FORESTRY

THE JOURNAL OF THE SOCIETY OF FORESTERS OF GREAT BRITAIN

Edited by R. W. V. PALMER

VOLUME XXIX : NUMBER 1

Price
Fifteen Shillings

Published by the
OXFORD UNIVERSITY PRESS
LONDON : GEOFFREY CUMBERLEGE
AMEN HOUSE, E.C. 4
1956

SOCIETY OF FORESTERS OF GREAT BRITAIN

THIS SOCIETY was formed at Aberdeen in 1925 and adopted its first Constitution at Oxford in 1926. This has been modified several times and the present Constitution became operative in December 1947.

The object of the Society is to advance and spread in Great Britain the knowledge of technical forestry in all its aspects. It is intended that the Society should be representative of the profession. Those not engaged in the practice of forestry or the allied sciences are cordially invited to join as Ordinary Members.

The activities include the publication of the journal, the holding of meetings, conferences, and excursions, and the awarding of a medal.

THE SOCIETY'S JOURNAL, called *Forestry*, is usually published twice a year, in January and July. It provides a means for the publication of the results of practice and research both in the growing of timber and in its utilization, including such basic sciences as forest physiology and ecology, forest soils, wood structure, and timber physics, and allied sciences such as forest entomology and forest mycology.

CONTRIBUTIONS may be accepted from members and others resident either in Great Britain or abroad. They should be sent to R. W. V. Palmer, Bannerleigh, Leigh Woods, Bristol. No article should be submitted which is being offered to any other journal for prior or simultaneous publication. Plates, figures, and tables should be used sparingly and their proportions designed to suit page dimensions, preferably, but not necessarily, for upright reading. Figures should be drawn large in black ink, preferably on Bristol board, and so as to allow appreciable reduction to page width without loss of clarity in the smaller details. Marginal lettering is best inserted in pencil. If graph coordinates are to be reproduced, graph paper with blue lines must be avoided. References to literature should be collected at the end of the paper, and arranged alphabetically according to author's name, and numbered. In the text each reference should be indicated by its number enclosed in brackets. Each article should begin with a summary which should be factual and convey briefly the content of the article and draw attention to all new information and to the main conclusions. It should be concise and should not normally exceed 200 words. It is understood that the author waives any copyright or translation rights in such summaries and that their reproduction in other publications will be permitted, subject to the source being duly acknowledged. Twenty reprints of the article will be sent free to each contributor and a reasonable number may be purchased by the contributor if ordered when the proofs are returned. The Society as a body takes no responsibility for the views expressed by contributors.

Forestry is sent free to members of the Society; others may register as subscribers by application to the Secretary, The Society of Foresters of Great Britain, 7 Albyn Place, Edinburgh, 2.

SOCIETY'S MEDAL. This may be awarded by the Society to any individual who has rendered eminent services to British forestry. Proposals for the award have to be made in the first instance to the Council by a Member of the Council. The regulations for the award will be found in Vol. XX, pp. 80, 81, and in Rule 11.

[*continued on inside back cover*

Forestry Commission

FIG. 1. Thornthwaite Forest, Lake District, Forest Workers-Holding on Comb Section, seen from the Whinlatter Pass. European larch, Douglas fir, and Sitka spruce

Forestry Commission

FIG. 2. Thornthwaite Forest, Lake District, thirty-year-old plantations of spruce and larch on the Hospital Fell, beside the Whinlatter Pass

PLATE I. Afforestation in the Lake District

THE DISCUSSION OF FOREST PROBLEMS

By W. E. HILEY

(*Presidential Address to the Society of Foresters, 18th May* 1955)

I HAVE been reminded by our Secretary that the Rules of our Society ordain that at the Annual General Meeting the President shall give a presidential address. This ordinance has not always been observed but, as a law-abiding citizen, I like to do my duty, and it happens that there is something I want to say.

I want to put forward the view that British forestry is likely to prove much less productive than it should be because we, in our generation, are neglecting some of the major problems of forest management, and are taking insufficient care to ensure that the techniques which we employ are appropriate to the country's needs. We are spending large sums of money in establishing forests, and it is our duty to ensure that the forest wealth which we create shall be as large and useful as we can make it. But I fear that we are neglecting many of the measures which might be most effective in securing this objective.

If any change is required in the orientation of our ideas, this Society is the body through which such a change should be inspired. We are the most highly trained foresters in Britain and we should lead in constructing a well-informed opinion on technical matters. At present we are failing to do this, and later in my address I shall advance some suggestions about the procedure which might enable us better to carry out this important function.

I am aware that some of the proposals about forest management which I have personally expressed are considered by many to be revolutionary, or at least, heretical. As I see them, these proposals are no more than an attempt by a plain, unprejudiced forester to build up an economic forest industry. They deal with some of the more urgent problems that confront us in our forest management; and though in some of the newer countries, especially South Africa and Australia, solutions to them are being eagerly sought, in Britain they are receiving less attention than they should.

I shall today mention only two of these problems. I would rather call them fields of ignorance, because they are matters in which our lack of knowledge prevents us from managing woodlands intelligently. I speak as a practical forester working in the south-west of England, and the knowledge which we there require may not be the same as is required in other regions. Nevertheless, I think the problems are widespread. But what are these fields of ignorance?

Firstly, I do not know how to thin plantations. Our most authoritative guide to thinning is contained in the 1951 edition of the Forestry Commission's pamphlet on *The Thinning of Plantations*; and the grades recommended in that pamphlet are used as a basis for the *Revised Yield Tables*. But inspection of the tables shows that, if we follow these grades, the trees of most species will grow in diameter very slowly during their later years, and that they will take an unnecessarily long time

to reach saw-timber size. If we thin more heavily, but not so heavily that the trees make less than six to eight annual rings to the inch outside the central knotty core, they will reach any desired size much more quickly. From a financial point of view this is a matter of great importance; and representative calculations appear to show that, if 4 per cent. interest is charged on capital, heavier thinning may save, on the average, something like 50 per cent. in the cost of growing trees 12 inches q.g.b.h. and larger. This would be a tremendous economy and to disregard it would be foolishness which verges on criminality. But we do not yet know enough about either our requirements, or the means of securing them, to design a rational thinning grade. On fertile sites we can grow trees much faster than this, but our knowledge of the relation of saleability of timber to growth rate is so scanty that I have incomplete confidence that this would be a justifiable risk.

I do not see that any of us can know how to thin plantations until we have made up our minds what kind of tree we want to grow, and have worked out how to grow it. As far as I can see all our present ideas about thinning schedules are based on traditions which have never been subjected to economic criticism, and on uninformed guesses.

Secondly, I do not know to what size we should try to grow our conifers, and until I know this I cannot think in terms of a working plan. Our difficulty here is partly due to the fact that in the south of England there is no regular market for conifers. Very few of our timber merchants really want them, because their mills have been designed to handle large hardwoods and they know little about the softwood trade. If they buy conifers they like the trees to be very large. There can be little doubt, however, that when more of the Forestry Commission forests are yielding trees of saw-timber size, new types of saw bench will be installed, and we may hope that, when such benches are handling a rapid through-put of logs of more or less standardized sizes, the cost of sawing may be only half as high as it is with the present hardwood benches. Mr. Gordon Jacob tells us that small logs can be sawn more cheaply per cubic foot than large logs, which is contrary to our present suppositions. I have not seen the evidence which would demonstrate the truth of this statement.

When we in Britain are producing a third of our coniferous requirements—and this is our avowed policy—home-grown timber will compete much more keenly than at present with imported timber. We must so organize our industry that the aggregate cost of producing sawn timber—growing, felling, extraction, sawing, and seasoning—will be as low as possible in relation to the price of comparable imported timber; and we must aim at producing those assortments in which we have the strongest competing power. For instance, it would be foolish to grow wood with very narrow annual rings, because such wood can be imported much more cheaply than it can be grown.

The investigations which are most needed in order to enable us to manage woods intelligently should be directed towards thinning grades and their relation to annual ring widths, the cost of growing trees under various conditions and with various ring-widths, the influence of ring width on the suitability of timber

for various uses, the cost of saw-milling in relation to tree size, and the value of output from trees grown in various ways and to various sizes.

I am sometimes told that these are matters for the distant future. Let us first grow our timber; we can then see how it can best be used. But surely this policy of first building up an enormous industry to produce a commodity, and only then finding out whether it is the most economical way of meeting consumers' needs, is opposed to all the principles of business management.

Others have told me that we cannot afford to thin heavily because we have to keep a large stock of timber in our forests against a possible emergency. This also seems to me to be a fallacious argument, because we need to grow saw-timber as fast as we can. If we follow the British Yield Tables we may have a fine stock of timber in 60 to 80 years time. But the need is urgent and we cannot wait so long. If we like to thin more heavily we can have a stock, albeit a lesser stock, of timber in 40 to 60 years. If it is even more urgent than that—and of course it is—we could grow it in even less time. But we should then need to set aside better land for forestry and to be content with broad-ringed timber. Perhaps we ought to do this. But I have seldom heard the subject discussed.

We are put to shame by a few progressive countries—and I would again mention South Africa and Australia—where, although their forest endeavour began later than ours, they are already far on the way to solving these problems. In Britain forest researchers have been so obsessed by immediate problems, especially nursery cultivation and the afforestation of difficult land, that we have never got round to these major issues, and I see little sign of any move in that direction.

I have mentioned only two among a large number of issues which vitally affect our forest industry. Some of the other problems are concerned with our national forest policy, others with the ambit of research, and others again with the curriculum at our forest schools. They are matters which concern us all, matters which we all want to discuss. This Society is the body which should provide a forum for discussion, and I hope that in the course of time it will so adjust its activities that it will not only provide a forum but will have such authority that any views it can collectively express will carry great weight.

The first step is to discuss, and I suggest that more time should be allowed for discussion at our meetings. As we are organized at present we have many discussions in the woods, but these are mostly concerned with silvicultural details that there confront us. During recent excursions we have devoted the last evening to a discussion which has always been entertaining and enlightening. But something better than the tag-end of a day could wisely be devoted to such an important object, and I shall endeavour to arrange that at our next excursion in Britain we should give it a more honourable place. I hope that members will think about this proposal and advance suggestions which can be discussed by the Council.

GEORGE LOYD COURTHOPE: AN APPRECIATION

By W. L. TAYLOR

The death of Lord Courthope on 2nd September 1955 leaves British foresters bereft of a wise counsellor and firm friend whose insight into the varied aspects of our rural life has been of outstanding value to the many public bodies on which he has served. Before his elevation to the Peerage he represented the Rye Division of Sussex in the House of Commons uninterruptedly for almost forty years and was known as an authority on forestry and agriculture.

The Rt. Hon. Sir George Loyd Courthope, Baron Courthope of Whiligh, in the peerage of the United Kingdom, Baronet, P.C., M.C., T.D., J.P., D.L., was born on 12th June 1877, the eldest son of G. L. Courthope, J.P., D.L., of Whiligh. His attachment to his ancestral home was evident to all privileged to visit him there. He was proud of his family's centuries old association with the history of Sussex: it being on record that a Courthope was M.P. for Hastings in 1400. It was, too, a matter of pride with him that Whiligh provided oak for the roof of Westminster Hall in the fourteenth century, and that he was able to offer oak timber for the repair of war damage to Westminster Palace after 1945.

George Courthope was educated at Eton and Christ Church and was called to the Bar by the Inner Temple. In 1906 he was elected Unionist Member for Rye. He served in Flanders in the First World War, being mentioned in despatches, wounded, and awarded the Military Cross.

He was Assistant Controller of Timber Supplies in 1917 and, among many other important public offices, was sometime President of the Royal English Arboricultural Society; Chairman of the Empire Forestry Association and of the Forestry Commission's Consultative Committee for England and a Forestry Commissioner.

A man of courage and staunch rectitude, Courthope was ever faithful to high principle: always ready to aid a cause he thought right and constructive. Of fine presence and courtly bearing, his keen eye would flash at any suggestion of insincerity. We shall all remember him with especial gratitude for his services to British forestry. His tie with the Forestry Commission was close: for many years he was the Commissioner's spokesman in the House of Commons. His wise counsel was of the utmost help to his colleagues in the difficult formative years of forest policy. For his conspicuous services, a Baronetcy was conferred on him in 1925. He was appointed to the Privy Council in 1937, and elevation to the Peerage followed in 1945.

One of the many graceful appreciations written by his friends to *The Times* describes Lord Courthope as one of the great gentlemen of our time. There could be a no more fitting tribute.

THE DISTRIBUTION OF MOISTURE IN THE LIVING STEM IN SITKA SPRUCE AND DOUGLAS FIR

By L. CHALK and J. M. BIGG

(*Imperial Forestry Institute, Oxford*)

SUMMARY

1. Equilibrium in the moisture content of the stem appears to be reached at a given percentage of saturation rather than at a percentage based on the dry weight, and this method of expressing moisture content eliminates many of the fluctuations apparent with the latter.
2. Summer moisture content in Sitka spruce (*Picea sitchensis*, Carr.) was highest on the site with the highest rainfall and lowest with the lowest rainfall. It decreased in late summer, suddenly in Sitka spruce (in August) and gradually in Douglas fir (*Pseudotsuga taxifolia* Brit.).
3. There was a sharp moisture gradient from cambium to heartwood, the saturated zone being very narrow except on the wet Sitka spruce site. In the Douglas fir it appeared that water could be withdrawn from the layers just behind the transpiration stream faster than it could be replaced, leaving this zone drier than the surrounding layers.
4. Lateral root pruning in Douglas fir led to the drying out of a narrow strip of tissue in the stem.

INTRODUCTION

THERE is some evidence that the amount of water available in late summer may be of critical importance for the formation of late wood in the conifers, particularly in Douglas fir (1, 2, 11) and it is possible that some of the variation in density of Sitka spruce grown in this country may be due to this factor. Lack of available water has also been suggested (4) as the cause of such defects as 'drought crack' and 'honeycombing' to which trees of Sitka spruce are prone in this country. It seemed, therefore, that it would be useful to find out whether any direct evidence could be obtained of changes in the moisture content of living stems at different times of the year and on different sites that would corroborate these hypotheses. Material of Sitka spruce was made available for this purpose by H.M. Forestry Commission from four sites, in Scotland, Wales, East Anglia, and southern England. A further investigation was made on Douglas fir and European larch to study the occurrence of small localized dry areas and the effect of branch stubs and of root pruning on the distribution of moisture in the stem.

MATERIAL

Sitka spruce, Picea sitchensis *Carr.*

The areas from which the Sitka spruce samples were collected were as follows: Gwydyr Forest in Caenarvonshire, representing a wet site, with a rainfall of 80 inches or more and a generally mild and damp climate, at an elevation of 800–900 feet; Swaffham Beat in the Thetford Chase area of Suffolk, representing a dry area with a rainfall of below 30 inches (average about 24 inches) and with a

high summer and a low winter temperature, at an elevation of 120 feet; the soil on this site, sand over boulder clay, is, however, unusually heavy for the Breckland area; Castlebank Wood, Drumtochty Forest in Kincardineshire, at an elevation of 750 feet; and Abbots Wood, Alice Holt Forest in Surrey, at an elevation of 300 feet.

The stands were all even-aged and three trees were selected from each site, a dominant, a tree of average size, and one of less than average size, referred to as the 'suppressed' tree. The details of these trees are given in Table I.

TABLE I. *Details of sample trees of Sitka spruce*

	Tree I	*Tree II*	*Tree III*
Gwydyr Forest, Bettws-y-Coed, age 23 years			
Height, feet	37	34·5	35
Girth, inches	26	19	15
Swaffham, Thetford Chase, age 25 years			
Height, feet	48	46	42
Girth, inches	32	23	17
Drumtochty, age 38 years			
Height, feet	57·5	58	54·5
Girth, inches	56	32	26
Alice Holt, age 27 years			
Height, feet	39	31	24·5
Girth, inches	24	15·5	11·5

Douglas fir, Pseudotsuga taxifolia *Brit.*

Seven trees (three dominants, one intermediate, and three suppressed) were selected from an even-aged stand 30 years old in Bagley Wood, near Oxford, growing over limestone. They ranged in girth from 12·5 to 35 inches. These trees were used mainly to study seasonal variation. Some other trees from Wytham Wood, near Oxford, were used for special purposes.

METHODS

The general method used was to extract a core from the standing tree with an increment borer; the core was then divided into predetermined lengths, and each length placed in a small glass tube sealed with a rubber cork. The holes in the tree were blocked with wooden pegs or with beeswax. The moisture contents were determined at the Imperial Forestry Institute in Oxford. The borings were made at approximately breast height and were repeated at intervals of about 3–4 weeks.

This method was recommended by Huckenpahler (8) in 1936 and was tested by Ranatunga in 1954 (12); the latter found that a rubber stopper gave a complete seal and that the method gave similar results to those obtained from large blocks, except that there was some indication that some moisture might be squeezed out from saturated samples by the pressure of the borer. As this point

is of some importance, a further investigation was made on a Douglas fir. Two disks of about 8 inches diameter were cut from the same tree and the moisture content was measured from four borings round each and from four segments spaced between the borings. The segments and cores were divided into 1-cm. lengths from the cambium. The results are shown below in Table II.

TABLE II. *Comparison of moisture contents obtained by increment borings and by segments from a disk*

	Distance from cambium, cm.				
	1	2	3	4	5
Disk No. 1	%	%	%	%	%
Point 1 Boring . . .	138	167	141	113	33
„ 2 Segment . . .	126	158	155	69	33
„ 3 Boring . . .	132	162	163	82	33
„ 4 Segment . . .	132	153	155	96	34
„ 5 Boring . . .	148	171	162	114	36
„ 6 Segment . . .	128	158	158	87	33
„ 7 Boring . . .	120	160	170	80	35
„ 8 Segment . . .	112	156	151	66	34
Disk No. 2					
Point 1 Boring . . .	137	175	133	52	33
„ 2 Segment . . .	139	166	105	63	34
„ 3 Boring . . .	114	174	130	52	33
„ 4 Segment . . .	140	169	141	56	31
„ 5 Boring . . .	137	174	129	77	32
„ 6 Segment . . .	140	180	127	63	31
„ 7 Boring . . .	114	174	129	53	33
„ 8 Segment . . .	138	169	127	75	32
Means of samples					
Disk No. 1					
Boring	135	165	..	..	..
Segment	125	156	..	..	..
Disk No. 2					
Boring	126	174	..	..	..
Segment	139	171	..	..	..

The figures in Table II do not confirm the tendency noted by Ranatunga in the outer and wetter samples. In disk 1, for example, the moisture contents of the outer centimetre are consistently higher in the boring, though usually lower in disk 2. In these samples the wettest part was the second centimetre and here there is less difference and the moisture content tends to be higher in the borings in both disks.

It was therefore concluded that borings give as accurate an assessment of moisture content as do segments, such as were used by Craib (3), and offer the great advantage over the latter method, of making possible successive samples from the same tree.

The amount of moisture in each sample was obtained by weighing it in its tube on arrival at the laboratory and subtracting from this the oven-dry weight of tube and specimen. The conventional moisture content was then expressed as a percentage of the oven-dry weight of the sample.

For reasons discussed later it was found necessary for certain purposes to express the moisture content as a percentage of the amount of moisture present at saturation. For this the cores were placed in water and subjected to a vacuum to extract as much air as possible and then left to soak in water till no further increase in weight could be observed. This took about 2 months, but the samples were left in water for approximately double this period. A drop of chloroform was added to each tube to prevent the development of moulds.

One of the difficulties of this method is to dry off the surface moisture consistently when obtaining the weight of the saturated sample. A technique was developed for this by rolling the cores lightly on filter paper. Three readings were taken for each sample; these were usually very close, but occasionally one reading differed markedly from the other two and was confirmed or rejected by repetition.

RESULTS

Significance of method of expressing moisture content

It is obvious that a light sample can hold more water at saturation than a dense one and that the difference will be exaggerated, if the moisture is expressed as a percentage of the dry weight, by the lower dry weight of the less dense sample. For comparative purposes it may be important to eliminate these differences in moisture content due solely to difference in density. This can be done by determining the saturated capacity of the wood and expressing the moisture present at any time as a percentage of that present at saturation.

The chief effect of using the percentage of saturation instead of the conventional percentage of moisture based on oven-dry weight was to reduce the apparent difference between fast-grown dominants and the smaller ('suppressed') tree from each group. A typical example of this in Sitka spruce is shown in Fig. 1, A and B. The conventional percentage of moisture shows the three trees separated in order of size, the largest having the highest moisture contents and the 'suppressed' distinctly lower values. This relation between dominance and conventional moisture content is very common not only in the Sitka spruce examined, but also in Douglas fir. The moisture contents of the same samples are shown in B expressed as percentages of saturation. It will be seen in B that there is very little difference between the three trees, though the 'suppressed' tree remains the driest. This is a typical result with Sitka spruce, but the 'suppressed' tree is sometimes distinctly the driest whichever method is used, as in the case of the broken line in Fig. 1, C and D. The same was found to be true of the Douglas fir samples. Using the percentage of saturation also tended to raise the value of the outer 2 cm. in relation to that of the middle 2 cm., as the wood was usually denser in the outer rings. This is illustrated in Fig. 1, C and D. A marked drop in the outer sample as illustrated in C is very common in both Sitka spruce and Douglas fir if the moisture content is expressed in the conventional way. In the Sitka spruce this apparent

anomaly usually disappears when the moisture is expressed as a percentage of saturation, as in D, in which it will be seen that the percentage of saturation is approximately the same (90 per cent.) for the first 4 cm. of the two dominants and then drops farther in, while in the 'suppressed' tree the moisture content decreases regularly from the outer and inner samples.

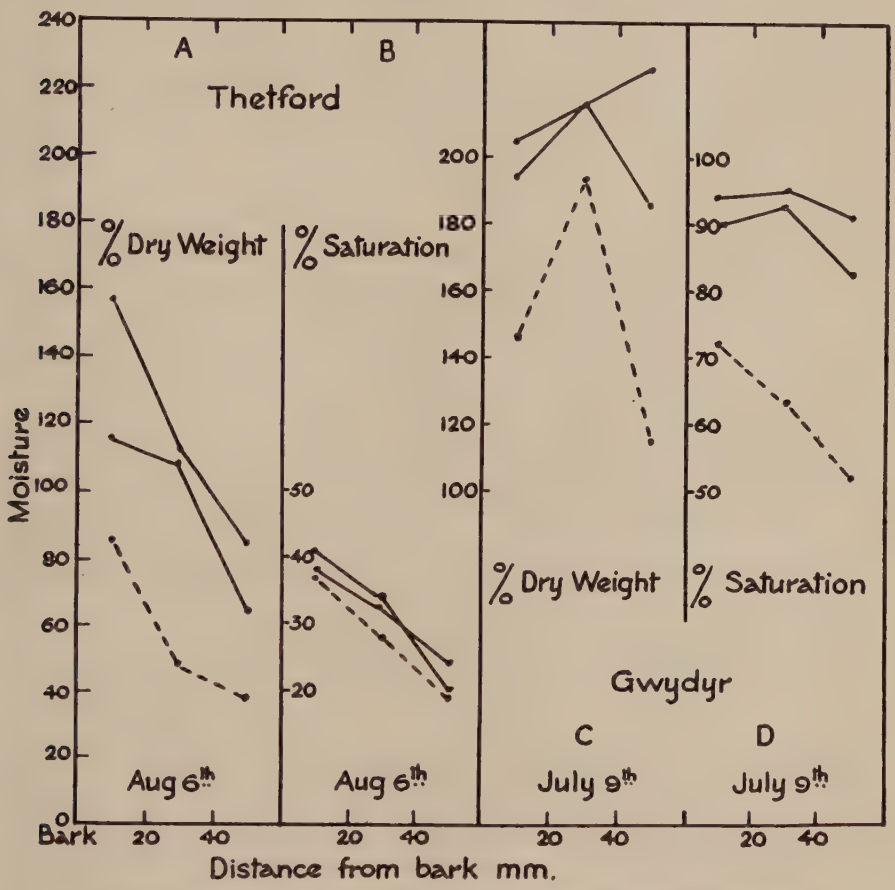

FIG. 1. Comparison of methods of expressing moisture content. Sitka spruce.

There is a similar levelling out of fluctuations in Douglas fir by using the percentage of saturation. It will be seen in Fig. 2, that not only is the apparent decrease in the moisture content at the outside reduced in A, but that in B, the converse is true, the apparent increase in moisture at the outside disappearing. In this tree the sapwood was very wide and the percentage of saturation was remarkably constant for the first 5 cm.

For most purposes of comparison, therefore, the percentage of saturation is the more suitable method. The orthodox percentage of moisture, however, has one advantage for certain purposes in that it gives an indication of the actual amount of water in the stem. Both methods have been used in the following investigation.

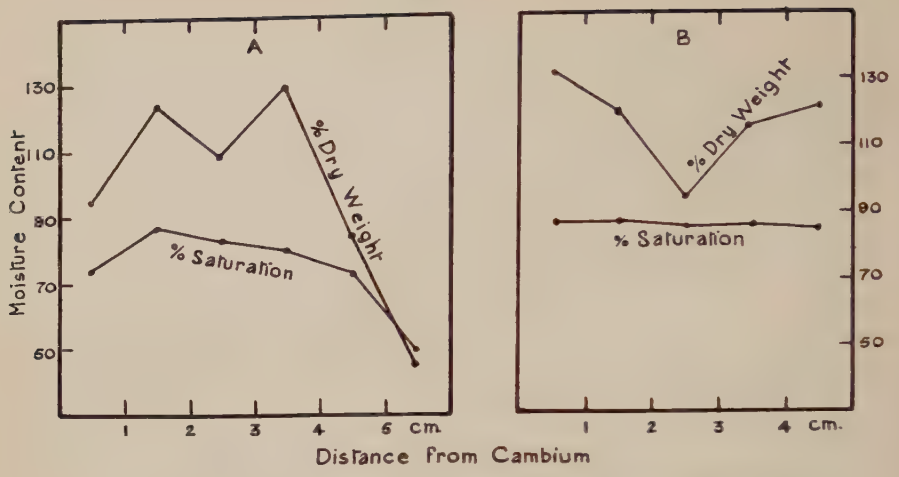

Fig. 2. Comparison of methods of expressing moisture content. Douglas fir.

Factors contributing to the typical pattern of distribution

Distance from the Cambium. In the Sitka spruce there was a marked general trend for the percentage of saturation to decrease from the outside to the edge of the heartwood, though occasionally the outer sample was slightly drier than the next.

The ranges for the dominants from all the sites in August–September were approximately as follows:

Outer 2 cm.	40–50	per cent.	of	saturation.
Middle „	30–40	„	„	„
Inner „	15–40	„	„	„

This type of gradient is present at all times of the year, though the trees contain much more moisture at some times than others, but it may be affected by the width of the sapwood and by conditions of growth. For example, in Fig. 3 the 'suppressed' trees (the broken lines) have consistently lower values than the dominants. Examples of the gradient in Sitka spruce when moisture is expressed as a percentage of saturation are shown in Fig. 3, in which the three sample trees for each site are shown separately for each area. These examples have been selected to illustrate particular points and the dates are not the same for each site. In Fig. 3, A and B the gradients have a characteristic form with a relatively sharp and regular decrease from the outer to the inner sample, and with the gradients in the 'suppressed' trees slightly below those of the larger trees. In the larger trees in C and D the wet area on the outside is more than 6 cm. wide and so the moisture content has not started to drop in the third sample taken. In D both Tree I and Tree II were larger, but in C Tree II was only 32 inches in girth compared with 56 cm. for Tree I. It is noticeable that with such very wet samples there always appear to be considerable fluctuations. In C, Tree I, the outer sample is distinctly

drier than the one 2–4 cm. inside. This drop in moisture content at the outside is common when the moisture content is expressed as a percentage of the dry weight, but is relatively rare when the percentage saturation is used. Similar gradients from cambium to heartwood occur in the Douglas fir, but a drop in moisture content in the outer sample similar to that illustrated in Tree I, Fig. 3, c, is both more common and more pronounced with the conventional moisture per cent. and is not entirely removed by using the 'percentage of saturation'. It is

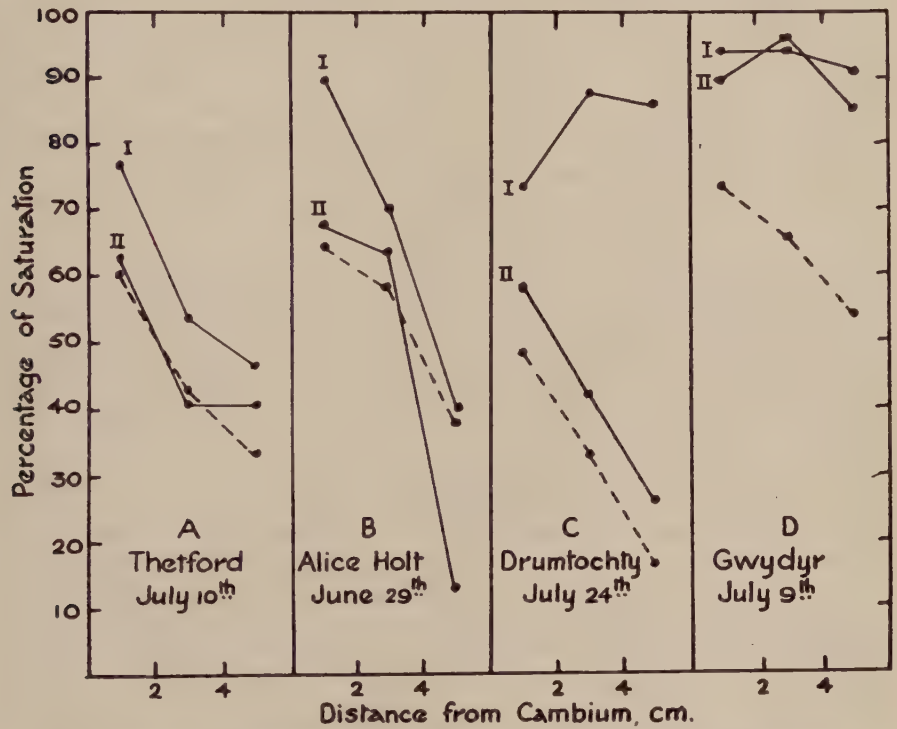

Fig. 3. Moisture gradient from cambium inwards, based on percentage of saturation.

usually assumed that the transpiration stream is carried by the outermost layer of the wood and that this layer is approximately saturated; it seemed possible, therefore, that the apparently contradictory result observed in the Douglas fir might be due to the use of samples that included too many rings. At various later sampling dates (July and November), therefore, extra borings were made adjacent to the routine ones and divided into 0·5-cm. samples instead of 1·0 cm. In every case, except in the suppressed trees, there was a rise in moisture percentage at the outside, even though the 1-cm. samples showed a fall. The suppressed trees presumably needed still smaller samples to show a rise. Two trees have been selected to illustrate this in Fig. 4. In B the rise in the outer half centimetre is very marked, with a very low value in the next sample. In A the rise at outside is only slight and at 70 per cent. is considerably lower than the percentage

(112 per cent.) reached at 2 cm. from the cambium. This relatively dry zone inside the cambium was characteristic of all the trees measured in this way.

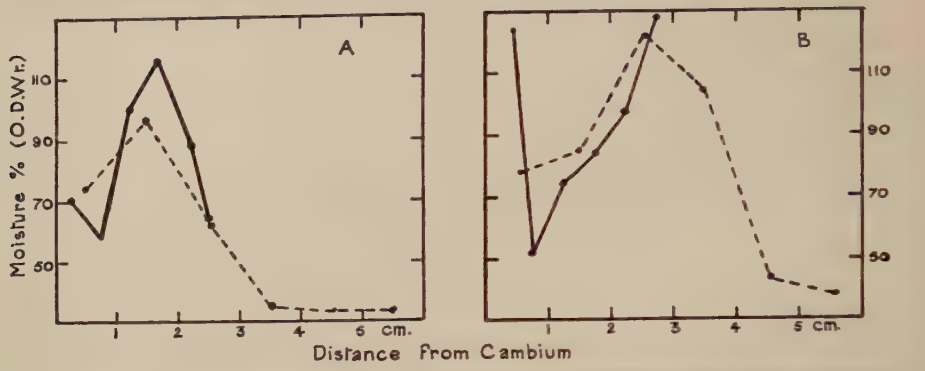

FIG. 4. Depth of sample and interpretation of moisture content of outer layers. Percentage of moisture based on dry weight.

Dominance. In the Sitka spruce samples dominance appears to be quite clearly related to a higher moisture content when this is expressed in the conventional way. It will be seen in Table III that the moisture content based on oven-dry weight (the columns marked *a*) shows a regular and marked decrease from Tree I, the largest dominant, to Tree III the 'suppressed' tree. With the percentage of

TABLE III. *Effect of dominance on amount of moisture and percentage of saturation. Sitka spruce sampled in August*

Site	*Tree I*		*Tree II*		*Tree III*	
	% *dry wt.* (*a*)	% *sat.* (*b*)	% *dry wt.* (*a*)	% *sat.* (*b*)	% *dry wt.* (*a*)	% *sat.* (*b*)
Gwydyr . . .	218	87	191	86	143	76
Thetford . . .	148	38	117	42	87	38
Drumtochty . .	178	50	112	35	63	21
Alice Holt . . .	150	51	135	49	115	43

saturation (the columns marked *b*) the differences between the trees are much less marked, though the sequence tends to remain the same. This can be shown more clearly by taking the moisture content of Tree I on each site as 100 and expressing that of the smallest tree as a percentage of this. The percentages based on oven-dry weight (columns *a*) range from 59 to 77 per cent., if the Drumtochty site is omitted, compared with 84–100 per cent. when expressed as the percentage of saturation (columns *b*). The Drumtochty site is exceptional in that Tree III has an unusually low moisture content expressed in either way and presumably was exceptionally short of water.

Season of the year. The Sitka spruce experiments were originally designed to find out whether there is any indication of changes of moisture content that might explain the poor development of late wood in this species under some

conditions. The period studied was therefore limited to the summer and autumn months, from the beginning of July to the beginning of October. The observations on Douglas fir covered the whole of the growing season and the first part of the winter.

The results obtained from Sitka spruce are summarized in Table IV and are illustrated in Fig. 5. In both the moisture content is expressed as the percentage of saturation. Fig. 5 illustrates very clearly the striking fall in moisture content that occurs on all the sites during August. This is perhaps slightly more marked on the wettest site (Gwydyr), and naturally tends to be less marked in the inner samples from the 'suppressed' trees, where these inner cores are approaching or possibly within the dry heartwood area.

It seemed possible that this drying out soon after the experiment was started might be in some way due to drying out of the holes, though these were stopped with wooden cores. In the Douglas fir investigation, in which the holes were sealed with beeswax, the stems started to dry out slowly at the beginning of August and continued to lose moisture until the end of December. This is illustrated in Fig. 6, using the conventional method of expressing moisture content. The large fluctuations in May and June cannot be satisfactorily explained and are possibly either the result of the development, in individual trees, of localized dry areas, which happen to have been sampled at these dates or of changes in density. No correlation with rainfall could be found.

In the Sitka spruce investigations the most striking difference between the trees from different sites is the high moisture content of the trees from Gwydyr. This can be seen clearly in the dominants in Fig. 5 and to some extent also the 'suppressed' tree. At the other extreme, the trees from Thetford are consistently the driest. For example, the July figures for outer 2 cm. of the two dominants at Gwydyr were 194–216 moisture per cent. representing about 94 per cent. of saturation compared with 114–84 moisture per cent. of 62–77 per cent. of saturation at Thetford. The corresponding figures for the 'suppressed' trees were 105 and 86 per cent. at Gwydyr and 95 and 60 per cent. at Thetford. The trees on the other two sites were intermediate.

Factors disturbing the typical pattern of distribution

Roots. A large root was removed in June from each of three trees of Douglas fir. Monthly borings were taken round these stems to find whether this treatment caused any changes in the pattern of moisture distribution. For 5 months no change was apparent, but in the sixth month (December) all the trees had developed a dry strip above the severed root of about the same width as the root. The method of sampling to determine the height of this strip proved unsatisfactory, and it can only be said with certainty that it extended for at least 3 feet 6 inches above the ground. This dry strip is illustrated for one of the trees in Fig. 7, where it can be seen that the cores from the second, third, and fourth centimetres have dried down to about 50 per cent. moisture content compared with 80–110 per cent. for the rest of the stem. Fig. 7 also shows clearly that,

TABLE IV. *Seasonal variation (July–October) in percentage of saturation in Sitka spruce grown on four sites*

Date	*Tree I*			*Tree II*			*Tree III*		
	Outer 2 cm.	*Mid. 2 cm.*	*Inner 2 cm.*	*Outer 2 cm.*	*Mid. 2 cm.*	*Inner 2 cm.*	*Outer 2 cm.*	*Mid. 2 cm.*	*Inner 2 cm.*
				Thetford					
1st July . .	..	..	..	..	..	..	76·5	41·2	34·0
16th July . .	76·8	53·5	46·4	62·5	40·5	40·5	60·2	42·8	33·2
6th Aug. . .	38·3	33·4	24·2	41·7	34·2	19·6	37·7	26·5	18·7
26th Aug. . .	45·0	30·2	20·1	41·2	36·1	20·6	38·6	29·2	15·1
17th Sept. . .	44·9	33·7	22·4	41·7	36·8	20·3	32·9	21·5	16·9
8th Oct. . .	48·7	44·3	28·4	46·4	40·0	21·0	31·2	25·4	15·7
				Gwydyr					
9th July . .	94·0	94·7	91·0	89·6	95·8	85·5	73·8	66·1	53·9
4th Aug. . .	86·8	91·3	81·4	85·6	93·3	65·6	76·1	66·3	34·6
24th Aug. . .	54·0	52·3	39·4	53·3	60·1	38·4	25·0	30·3	17·9
14th Sept. . .	41·5	53·1	38·8	48·1	59·7	39·9	39·0	26·2	22·7
5th Oct. . .	50·9	60·7	50·7	49·1	53·1	33·7	44·6	48·9	30·2
				Drumtochty					
3rd July . .	71·0	89·0	87·2	46·1	44·1	18·5	48·2	36·9	..
24th July . .	73·7	88·4	85·5	57·9	42·0	26·3	48·5	32·9	16·6
13th Aug. . .	50·3	59·0	31·1	35·1	27·5	16·3	21·0	12·8	10·8
4th Sept. . .	45·0	53·9	54·6	31·5	27·6	22·3	27·9	15·3	9·2
25th Sept. . .	42·9	54·6	56·1	32·8	16·9	19·7	34·6	16·0	16·8
				Alice Holt					
29th June . .	90·0	70·0	39·1	67·6	63·7	13·3	64·4	58·4	38·0
20th July . .	80·1	79·8	24·8	64·6	26·0	24·5	78·0	63·7	51·7
10th Aug. . .	51·3	52·8	22·5	49·0	42·3	16·8	43·0	39·2	17·7
31st Aug. . .	53·0	49·8	17·8	47·9	20·6	16·7	47·0	41·0	18·3
21st Sept. . .	51·8	26·5	16·7	39·0	20·1	9·5	46·5	28·4	25·5
12th Oct. . .	55·3	48·9	20·1	56·7	31·7	15·6	42·8	24·5	20·4

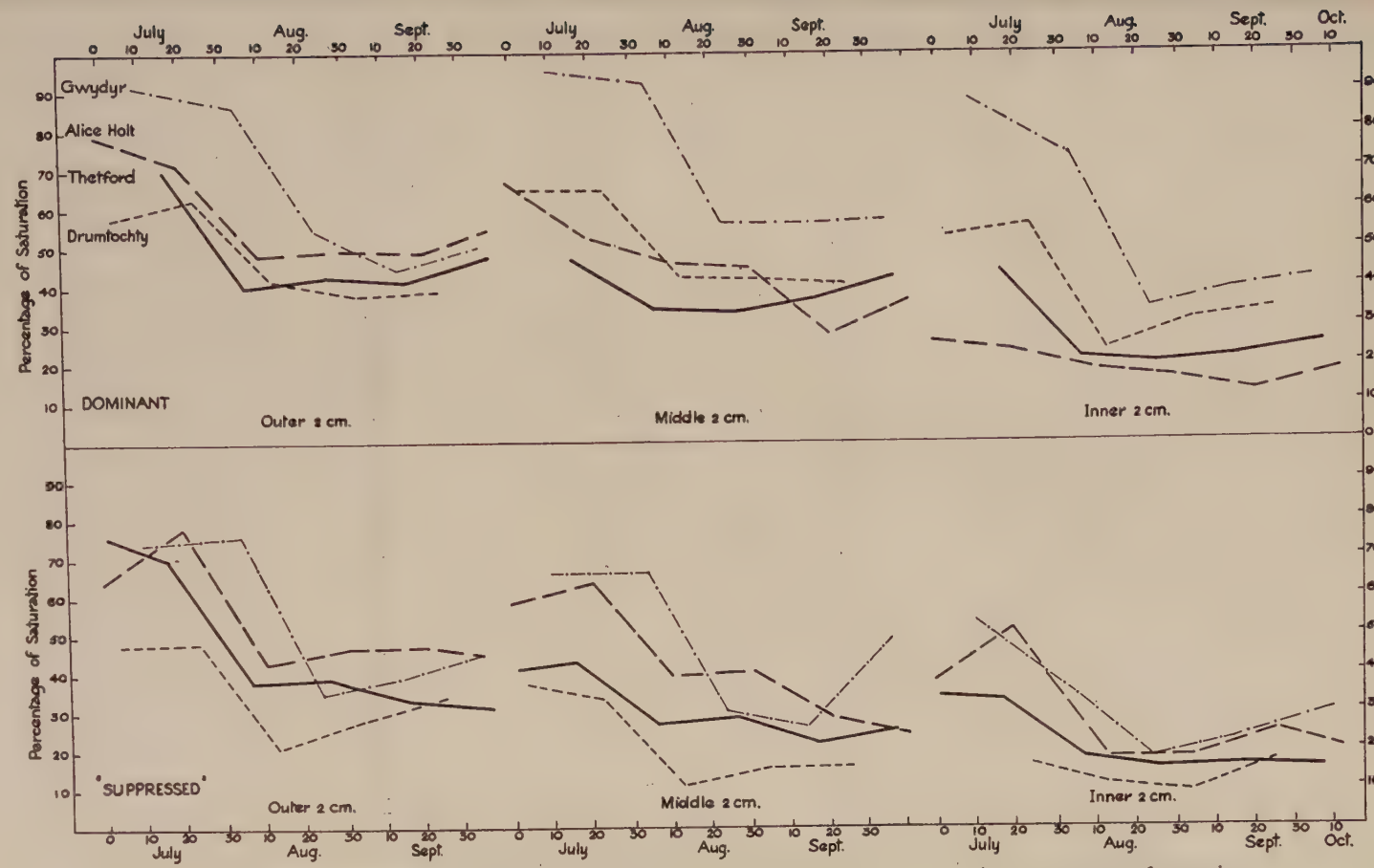

FIG. 5. Seasonal variation and distribution of moisture content in Sitka spruce on four sites. Percentage of saturation.

contrary to what might be expected, the outermost centimetre remained unaffected. The innermost layer at 4–5 cm. was also unaffected, but this was very dry (about fibre saturation point) and probably coincided with the outer heartwood.

Dead branches. An attempt was made to determine the effect of removing the

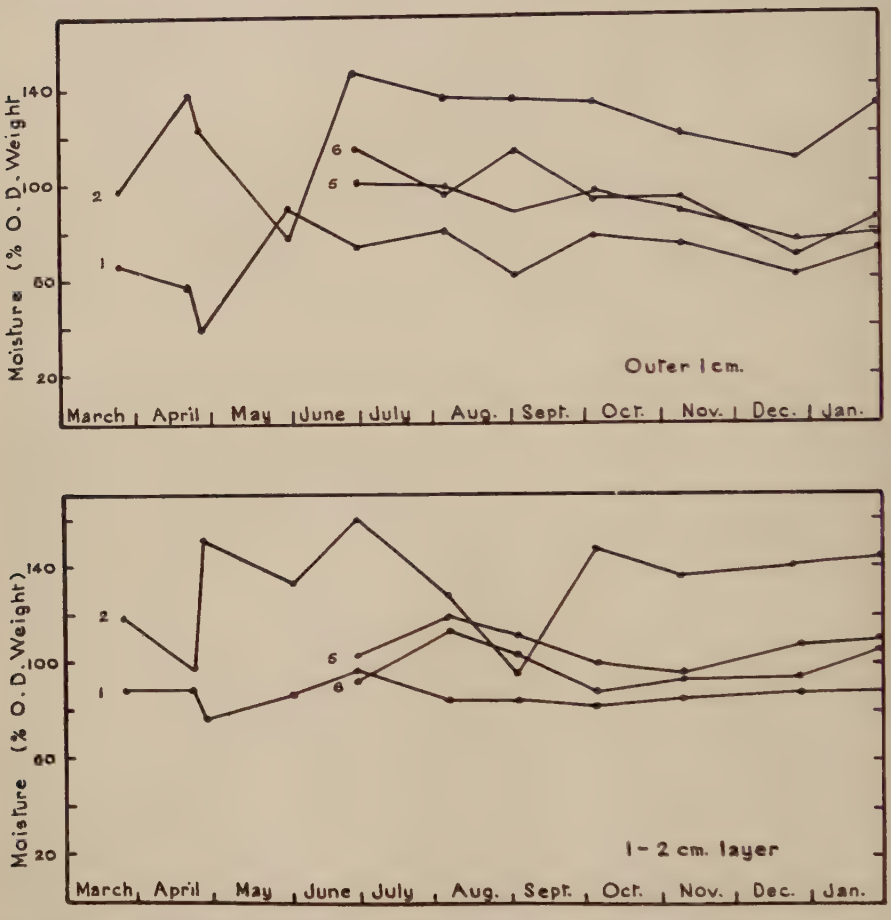

Fig. 6. Seasonal variation and distribution of moisture content in Douglas fir. Percentage of dry weight.

dead branches on the moisture content of the stem of European larch, *Larix decidua* Mill. This investigation was carried out before the importance of expressing moisture content was fully appreciated and some of the material was destroyed. There was some indication that the conventional moisture content of the main stem is reduced by 2–4 per cent. in each of the three 2-cm. layers, but that the percentage of saturation in the branch stubs themselves is reduced only in the outer 2-cm. layer. This point and the difference between the results obtained by the two methods are shown in Table V.

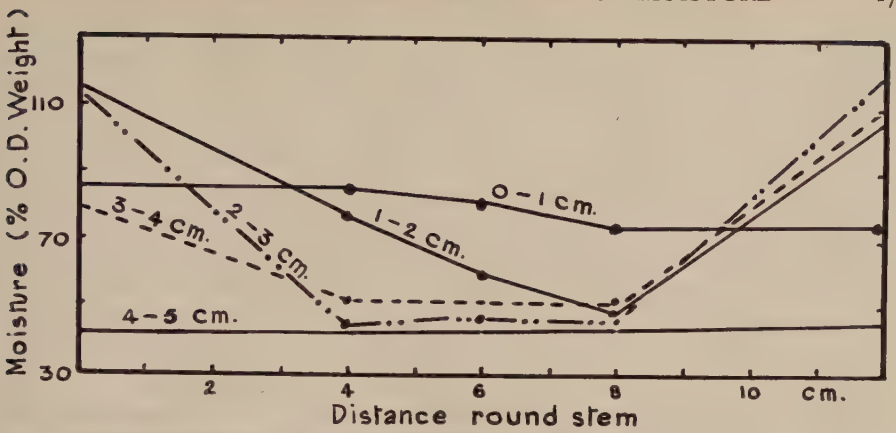

FIG. 7. Moisture distribution in stem at 3 feet 6 inches above ground five months after severance of large lateral root. Douglas fir.

TABLE V. *Moisture content of two branch stubs and surrounding wood expressed as* (a) *percentage of oven-dry weight and* (b) *percentage of saturation. Branch stubs in italics*

Depth of sample	*Position*	(a) *Moisture content % dry weight*	(b) *Moisture content % saturation*
0–2 cm. . .	Stem	56	53
2–4 cm. . .	Stem	46	44
4–6 cm. . .	Stem	49	49
0–2 cm. . .	Branch	*22*	*37*
2–4 cm. . .	Branch	*23*	*45*
4–6 cm. . .	Branch	*30*	*53*
0–2 cm. . .	Stem	60	57
2–4 cm. . .	Stem	50	54
4–6 cm. . .	Stem	50	48
0–2 cm. . .	Stem	56	55
2–4 cm. . .	Stem	50	52
4–6 cm. . .	Stem	47	41
0–2 cm. . .	Branch	*22*	*39*
2–4 cm. . .	Branch	*27*	*48*
4–6 cm. . .	Branch	*37*	*75*

DISCUSSION

One of the most interesting results of this investigation has been to emphasize the importance, for purposes of comparison, of expressing the amount of moisture in the stem as a percentage of the amount of moisture held at saturation. It is customary in investigations concerned with timber to express the moisture content as a percentage of the dry weight of the sample. This is satisfactory for

moisture contents at about the so-called fibre saturation point or lower, as the water is limited to that present within the cell walls themselves and reaches equilibrium under any particular conditions at a given percentage of saturation of the cell wall. In the wetter parts of the living stem, however, most of the moisture is present as free water in the cell lumina and intercellular spaces and appears to reach equilibrium at a given percentage of saturation of the whole cell or block of wood. The difference between the two methods of expression is chiefly of importance in connexion with changes in density. For example, if a light and a dense sample are compared under conditions of equilibrium, below the fibre saturation point the specimens will have the same conventional moisture content (expressed as the percentage of the oven-dry weight), though the dense wood will contain a greater quantity of water; at well above the fibre saturation point the percentage of saturation would be the same in both specimens, but the conventional moisture contents would be different, the denser wood having a lower conventional percentage of moisture. The use of the conventional method may thus indicate apparent trends of variation within a stem that are nothing more than the result of changes in density. For example Nylinder (10) has shown that in *Pinus sylvestris* the conventional moisture content of the outer sapwood steadily increases upwards in the stem, rising from about 130 per cent. at the base to 180 per cent. in the upper part of the stem; but, expressed as a percentage of saturation, the moisture content was almost constant at 85 per cent. all the way up the stem. He found also that the moisture content traced upwards in the stem evened out in a similar way in Norway spruce, and at almost the same figure, when expressed as the percentage of saturation. In spite of this, however, Nylinder bases his main conclusions on the conventional moisture content. In the present investigation also it was found that many of the differences apparent with conventional moisture percentage disappear if the percentage of saturation is used and that quite a different picture of moisture distribution may then be presented.

Seasonal changes in moisture content have been studied by various authors, and it seems to be generally agreed that moisture in the sapwood tends to be lowest in the middle, or towards the end, of the growing season and highest at some time in the winter. Craib (3) pointed out that in the resinous conifers the heartwood is dry and remains unchanged throughout the season of growth and this has been confirmed by other authors.

In the present investigation the changes in the Douglas fir are generally similar to those found by other authors and call for no special comment. In the Sitka spruce there was a sharp drop in the moisture content (percentage of saturation) in August, which bore no apparent relation to the weather. For example, the samples showing this drop in the Gwydyr trees on the 24th August were sent with the comment that they were collected during a very wet spell. A sudden decrease in moisture occurring at approximately the same date in such widely separated districts might conceivably be due to some physiological rhythm, such as the development of maximum transpiration by the new crown at a certain period in the growing season, or it might perhaps be an accident due to the experimental

procedure. It is noticeable that the decrease occurred at the third sampling on each site, which might suggest some connexion with the removal of the cores, though it should be remembered that the third sampling was taken at approximately the same date on each site. The holes from which the borings were taken were sealed after the core had been removed, so that there was little likelihood of any actual loss of moisture from the wound, but the removal of the core may have let in air by breaking the water columns in the manner suggested by Greenidge (7) in connexion with the distribution of injected dyes after root pruning. Both Greenidge's experiments and those on the Douglas fir suggest, however, that any such entry of air would be limited to a very narrow strip above and below the wound, so that the third sample taken at right angles round the stem should almost certainly be from an area unaffected by the two previous borings. More direct evidence against the hypothesis that the decrease in moisture content was due in some way to the borings can be obtained from the absence of any similar sharp drop in the Douglas fir, in which the summer decrease in moisture content was very gradual. Nevertheless this unusual behaviour of Sitka spruce must remain to some extent suspect till confirmed by further experiments.

An increase in moisture content in winter has been observed by Nylinder (10) in Scots pine and Norway spruce and by Gibbs (6) in *Tsuga canadensis* Carr. In both the Douglas fir and the Sitka spruce there was some evidence of increasing moisture content at the end of the year, but the change was comparatively slight, e.g. 40–50 per cent. of saturation rising to 48–56 per cent. in the Sitka spruce by the end of October. The rise at the end of the year in the conventional moisture content in Douglas fir was of the same order as that found by Nylinder in Scots pine and Norway spruce. It may be noted that Gibbs (6) found little seasonal change in species of *Abies*, *Picea*, and *Pinus*.

It is generally believed that the transpiration stream may be limited to a very narrow zone, possibly only the outer one or two growth rings, and this is borne out generally by the gradients observed in the Douglas fir and Sitka spruce. In the two larger trees of Sitka spruce from the site with the high rainfall (Gwydyr) there was a zone of at least 6 cm. of almost saturated wood in the outer sapwood, and even in the 'suppressed' tree the moisture decreased inwards only very gradually. On the other sites the percentage of saturation of the outer 2 cm. was always higher in the larger stems and lowest in the smallest tree, implying a wider zone of saturated wood in the larger trees. Fielding (5) has noted that in *Pinus radiata* the moisture content (per cent. o.d. wt.) tends to be higher in the dominants and higher in trees of fast growing stands than that of trees of the same age on poorer sites. Nylinder (10) also has found that moisture content rises with increasing diameter in the same age class (Scots pine and Norway spruce). The higher percentages of saturation in the outer sapwood of fast-grown trees implies a smaller proportion of air and it is possible that this may be connected with the smaller proportion of heartwood that is usually associated with such trees.

Changes in the regular pattern of the distribution of moisture, such as have been described above, particularly those associated with drying out, are of interest in connexion both with the general water-conducting system of the tree and with

the occurrence of defects attributed to shortage of water. In the Douglas fir it was observed that the percentage of moisture in the outer sample was commonly lower than that of the middle one, and similar lower moisture contents in the outer samples can be seen in Craib's curves for *Taxus* and *Chamaecyparis* (3). Though this can no doubt be partly explained by assuming a higher density in the outer layers, this is probably not the whole explanation, as a similar phenomenon was sometimes observable in the Sitka spruce when the moisture was expressed as the percentage of saturation. The experiments with smaller samples of Douglas fir showed that this apparently drier outer zone consists of a narrow saturated layer on the outside, with a drier zone immediately within it (see Fig. 4), suggesting that if the rate of transpiration temporarily exceeds that of the intake by the roots, the deficit is met by the layers immediately inside the saturated layers of the transpiration stream. The point of interest here is the suggestion that such zones may have water withdrawn from above faster than it can be replaced radially from within the stem. A relatively slow radial movement of moisture has been deduced from the spread of dyes in living stems. Roach (13), for example, estimated the movement of water vertically, tangentially, and radially as in the proportion of 100: 10: 1. It seems therefore very probable that any sudden shortage of water in the tree, such as might occur on a shallow soil, might lead to collapse in the full cells of the outer ring, as water is drawn off from above, leading to the development of 'honeycombing' such as has been described by Day (4) and by Lutz (9).

There is some evidence to show that round the stem there may be drier strips or patches, and it has been shown above that severance of a lateral root may lead to the development of a narrow strip of drier wood above the root. Greenidge (7) found that cutting a root affected the distribution of injected dyes, there being an unstained strip above any root that had been severed. He concluded that this was the result of fracturing the water columns and thus permitting gas to enter the conducting elements. It may be of some significance that Greenidge observed this reaction to root-pruning of sugar maple after 20 days, whereas with Douglas fir it took about 5 months before any noticeable change developed in the moisture content of the stem.

The direct evidence that severance of a root can lead to lower moisture percentages in a narrow strip above the root may be of significance in connexion with the development of the 'drought cracks' described by Day (4), which appear to follow the same course as the dry strip above a severed root. Though drought cracks are usually associated with soils of limited capacity for holding water, Day notes that they may occur on sites where undue limitation of water is unlikely. Possibly under such conditions damage to a particular root may cause a strip of the stem to dry out sufficiently to cause collapse of the early wood tracheids and the development of a drought crack.

ACKNOWLEDGEMENTS

The authors are indebted to the Research Branch of the Forestry Commission for supplying the material of Sitka spruce and in particular to Messrs. J. Campbell,

W. MacDonald, G. Pringle, and R. Taylor, who made and dispatched the increment borings and to Mr. M. V. Laurie and Dr. F. C. Hummel for their help and advice in organizing the collection of the material. Thanks are also due to St. John's College, Oxford, for the material of Douglas fir collected in Bagley Wood.

LITERATURE REFERENCES

(1) Chalk, L.: *The Formation of Spring and Summer Wood in Ash and Douglas Fir.* Oxford For. Memoir, No. 10, pp. 48 (1930).

(2) —— 'Water and the Growth of Wood of Douglas Fir.' *Quart. J. For.* xliv. 222–33 (1951).

(3) Craib, W. G.: 'Regional Spread of Moisture in the Wood of Trees, III, Notes,' *R. bot. Gdns., Edinburgh*, lxvi. 1–8 (1923).

(4) Day, W. R.: *Drought Crack of Conifers.* For. Comm. For. Rec. No. 26, pp. 39 (1954).

(5) Fielding, J. M.: 'The Moisture Content of the Trunks of Monterey Pine Trees.' *Aust. For.* xvi. 3–21 (1952).

(6) Gibbs, R. D.: 'Seasonal Changes in Water Contents of Trees.' *Proc. 7th Intern. bot. Congress*, 1950, Stockholm, p. 230.

(7) Greenidge, K. N. H.: 'Studies in the Physiology of Forest Trees, II. Experimental Studies of Fracture of Stretched Water Columns in Transpiring Trees.' *Am. J. Bot.* xlii. 28–37 (1955).

(8) Huckenpahler, B. J.: 'A Comparison of Several Methods of Making Moisture Determinations of Standing Trees and Logs.' *J. For.* xxxiv. 165–8 (1936).

(9) Lutz, H. J.: 'Occurrence of Clefts in the Wood of Living White Spruce in Alaska.' *J. For.* l. 99–102 (1952).

(10) Nylinder, P.: 'Über die Verteilung von Rohwichte und Holzfeuchtigkeit in Kiefern- und Fichtenstämmen und ihre Bedeutung für die Flößerei in Schweden.' *Holz als Roh- u. Werkstoff*, xi. 354–61 (1953).

(11) Paul, B. H., and Martz, R. O.: 'On Controlling the Proportion of Summerwood in Longleaf Pine.' *J. For.* xxix. 784–96 (1931).

(12) Ranatunga, M. S.: *Methods of Measuring Moisture Content in Living Stems.* Thesis. Oxford, 1954.

(13) Roach, W. A.: *Plant Injection for Diagnostic and Curative Purposes.* Tech. Comm. Imp. Bur. Horticulture, No. 10, pp. 78 (1938).

THE COMPOSITION OF TREE LEAVES

By J. D. OVINGTON

(The Nature Conservancy, Merlewood, Grange-over-Sands)

SUMMARY

Tree leaves have been collected from three series of forest plots, each series with a wide range of tree species established on a fairly uniform soil type. The contents of sodium, potassium, calcium, magnesium, iron, manganese, silica, phosphorus, ash, carbon, and nitrogen in the tree leaves are given. The chemical compositions of the leaves are related to soil conditions and the tree species selected for afforestation. When hardwood leaves are compared with softwood leaves some consistent differences in chemical composition occur between the two groups at all three localities. The ecological and silvicultural applications of foliar analysis are considered.

INTRODUCTION

A CONSIDERABLE quantity of plant nutrient is taken up annually by tree roots and a proportion of this is returned to the soil as leaf-fall each year. In this way a redistribution of nutrients in the soil profile occurs and the amounts concerned in this transfer depend upon the weight and composition of the leaf-fall. The chemical composition of tree leaves should, therefore, be of interest to foresters since it gives some indication of the quality of the organic material falling on the forest floor and governs, to some extent, the process of decomposition. Foliar analysis of the trees comprising the standing crop may also be useful in interpreting the general availability of plant nutrients in a forest soil and be a valuable tool to the forester, who has to select the most suitable tree species to follow an existing woodland. Agronomists have found that the nutrient contents of agricultural crops are frequently related to soil conditions (3). Leyton (5) has suggested that some caution is required in the interpretation of tree leaf analysis since such factors as the growth of the trees and total leaf weight should be taken into account. Compared with some European and American countries, relatively little foliar analysis of trees has been reported in this country. In the present paper the results are given of leaf analysis from trees growing at three different localities in Great Britain, namely, West Tofts, Bedgebury, and Abbotswood.

The soil at West Tofts, in Thetford Chase, is a calcareous sand, whilst the soils of Bedgebury in Kent, and Abbotswood in the Forest of Dean, are acid and have originated from the Hastings Beds of the Tunbridge Wells Sandstone and the Old Red Sandstone respectively (8). So far as is known, at the time of planting soil conditions were fairly uniform over each locality and no fertilizers were ever applied to the plantations. With a few exceptions the whole of each series of plots was planted in one year so that the trees at each locality are of similar age although differing considerably in size. In general, all of the plantations which have been sampled have grown satisfactorily and have closed canopy.

METHODS

There are some inherent difficulties in applying the results of foliar analysis to

forestry problems. Numerous observers have found that the composition of tree leaves is not constant but changes during the period that the leaves remain on the trees (1, 2, 6, and 7). In addition the chemical composition of the leaves not only differs in successive years (12) but also varies with position in the crown (13, 14).

To minimize some of these difficulties the leaves from each locality were all collected at the same time and the three localities were sampled as quickly as possible in late summer; West Tofts in 1950 and the other two in 1951. Usually a separate bulk sample of leaves from each of five random trees was collected in each plot. It is extremely difficult, particularly for tall trees such as those at Abbotswood, to collect a truly representative sample of leaves, but every effort was made to ensure this by gathering a large bulk from as much of the canopy as possible. The leaves from each tree were thoroughly mixed and a random sample taken.

The samples were transported to the laboratories in waterproof bags and quickly dried before grinding in a Christy and Norris mill so as to pass through a sieve with an aperture of 0·4 mm. Some iron may have been added to the leaves in the process of grinding (4). The wet digestion method for ashing as described in Piper (11) using nitric, perchloric, and sulphuric acids was followed and the mineral elements were determined in the resultant solution. Organic carbon was determined by the Walkley and Black method and nitrogen by the micro-Kjeldahl technique.

THE PERCENTAGE COMPOSITION

The percentage composition of the elements which have been determined are given in Tables I, II, and III.

When each locality is considered as a whole, the percentages of sodium, potassium, magnesium, iron, silica, carbon, and nitrogen are broadly similar for all three localities, but in contrast, differences in the phosphorus, calcium, and manganese contents occur. These differences seem to result from inherent differences in the characteristic soil conditions of the three localities. The amount of exchangeable phosphorus in the soil at Bedgebury, for instance, is small and the tree leaves are correspondingly poor in this element. The soil at West Tofts is particularly rich in calcium, containing free particles of calcium carbonate, and the tree leaves collected there contain more calcium than those from the other two localities. The relatively low contents of manganese in the leaves at West Tofts probably reflect a smaller uptake of manganese by trees growing on an alkaline soil. The uptake of iron, like that of manganese, may be modified on alkaline soils, and the uniformity in the percentages of iron may be a result of the pollution of samples during the grinding process.

Over each locality, great variation occurs in the chemical composition of the leaves depending largely upon the tree species which has been sampled. More extensive sampling of an individual species from a wider variety of soil types would be necessary to define precisely the natural limits of the nutrient content in the leaves. The relationships existing between the composition of tree leaves and the corresponding soil conditions are complex, since under certain conditions elements may be accumulated in excess of normal requirements. Nevertheless,

for the various tree species of the three experimental areas, it is possible to recognize some general features of leaf composition. Thus, of all the conifers, larch, and Douglas fir tend to have the greatest nutrient content, whilst the needles of both Scots and Corsican pine are generally low in nutrients. The leaves of *Thuja plicata* and *Chamaecyparis lawsoniana* are particularly rich in calcium and it is noteworthy that their leaves and litter layers have the highest pH of the Bedgebury plantations (Ovington (8)).

Comparisons are frequently made between hard and softwoods and for convenience the plantations have been grouped in this way in the tables. Great dissimilarity in leaf composition, particularly in the softwoods, occurs within each of the two groups and there is no consistent difference between hard and softwoods for the calcium, iron, and silica contents of the leaves at the three localities. Chandler (2) has emphasized that not all coniferous leaves are low, and not all deciduous trees are high in calcium. He considers that the relative order of tree species with respect to calcium content does not change greatly for different areas.

Despite this variation within the hardwood and softwood groups, at each locality there are noteworthy differences for the remainder of the elements which have been determined. Thus, the percentages of potassium and nitrogen in the hardwood leaves are all greater than for any of the conifers. Similarly more magnesium is contained in the hardwood leaves, only the oak leaves of the mixed plantation at Abbotswood containing less magnesium than the conifer leaves. This hardwood plantation is outside the Abbotswood experimental block and the soil conditions differ to some extent from the rest of the sampling area. A higher percentage of phosphorus is present in the hardwood leaves than in the leaves of the corresponding evergreen conifers. The leaves of larch, which is deciduous, are, however, more comparable in content of phosphorus, to the leaves of hardwoods than to the other conifers. The relatively large percentage of phosphorus in larch needles is very characteristic and it is interesting that both the associated ground floras and the mineral soil in the larch stands also have an increased phosphorus content. In contrast, when comparisons are made of the carbon percentages in the leaves, conifers have the greatest percentages at each locality. The sodium and manganese percentages also tend to be higher in the leaves collected from the conifers. No hardwood leaves, for instance, were recorded as having a sodium content greater than 0·05 per cent., but six of the seventeen stands of conifers have percentages greater than this.

DISCUSSION

The dry weight of leaf produced each year by a well-stocked forest stand is approximately 3,000 lb. per acre, depending upon the specific tree species that has been established. Of this leaf material, the mineral elements that have been determined account on an average for about 4 per cent., whilst carbon and nitrogen represent a further 60 per cent. The total quantity of nutrient contained in the tree leaves, and hence in the leaf-fall, from a close plantation is considerable, although the quantities will vary according to the tree species and site conditions.

These plant nutrients are returned to the forest soil in the leaf-fall each year, but within the same period an equivalent amount must be absorbed by the trees from the soil and incorporated as new leaf material. This nutrient cycle between the soil, trees, and leaves, results in the deposition of considerable quantities of nutrients on the forest floor and the enrichment of the upper soil horizons. The magnitude of the cycle gives some indication of the high rate of nutrient turnover in forest soils, but in addition nutrients are also being incorporated in the branches and boles of the trees, and there is some loss by leaching. Little is known of the part played by the breakdown of the leaf material in promoting the release of nutrients from the mineral soil particles.

Whilst the chemical composition of tree leaves depends partly upon site conditions, it is largely a characteristic of the individual tree species since great differences occur between species growing under comparable soil and climatic conditions. Leaf material represents a large proportion of the litter and humus horizons of forest soils, so that differences in the chemical composition of the leaves are reflected in the varying degrees to which soil conditions are modified by different tree crops. The leaves of hardwoods and softwoods tend to be distinct in chemical composition, and there are corresponding differences in the accumulation of the surface organic layers and in profile development (Ovington (9)).

ACKNOWLEDGEMENTS

I am grateful to the Forestry Commission for allowing me to take samples in their forest plantations and for assistance given during the course of the investigation.

LITERATURE REFERENCES

(1) Alway, F. J., Maki, T. E., and Mathley, W. J.: 'Composition of the Leaves of Some Forest Trees.' *Bull. Amer. Soil. Surv. Ass.* xv. 81 (1934).

(2) Chandler, R. F. Jr.: *The Calcium Content of the Foliage of Forest Trees.* Corn. Univ. Agric. Expt. Sta. Mem. 228 (1939).

(3) Goodall, D. W., and Gregory, T. G.: *Chemical Composition of Plants as an Index to Their Nutritional Status.* Imp. Agric. Bur. Tech. Comm. 17 (1947).

(4) Hood, S. L., Parks, R. Q., and Hurwitz, C.: *Mineral Contamination from Grinding Plant Samples.* Indust. Eng. Chem. (Anal. ed.), xvi. 202 (1944).

(5) Leyton, L.: *The Growth and Mineral Nutrition of Spruce and Pine in Heathland Plantations.* Imp. For. Inst. Paper 31. University of Oxford (1954).

(6) McHargue, J. S., and Roy, W. R.: 'Mineral and Nitrogen Content of the Leaves of Some Forest Trees at Different Times in the Growing Season.' *Bot. Gaz.* xciv. 381 (1932).

(7) Mitchell, H. L.: *Trends in the Nitrogen, Phosphorus, Potassium and Calcium Content of the Leaves of Some Forest Trees during the Growing Season.* Black Rock Forest Papers, i (1936).

(8) Ovington, J. D.: 'Studies of the Development of Woodland Conditions under Different Trees. 1. Soils pH.' *J. Ecol.* xli. 13 (1953).

(9) —— 'Studies of the Development of Woodland Conditions under Different Trees. 2. The Forest Floor.' Ibid. xlii. 71 (1954).

(10) —— 'Studies of the Development of Woodland Conditions under Different Trees. 5. The Mineral Composition of the Ground Flora.' To be published later.

(11) Piper, C. S.: *Soil and Plant Analysis.* Monograph from the Waite Agricultural Research Institute, Adelaide, Australia (1950).

(12) Plice, M. J.: 'Uptake of Minerals by Trees in successive years.' *Proc. of the Oklahoma Acad. of Sci.* 24B, 60 (1944).

(13) Serex, P. Jr.: 'Plant Food Materials in Leaves of Forest Trees.' *Jour. & Proc. Amer. Chem. Soc.* xviii. 326 (1954).

(14) White, D. P. 'Variations in the Nitrogen, Phosphorus and Potassium Contents of Pine Needles with Season, Crown Position and Sample Treatment.' *Soil Sci. Soc. Amer. Proc.* xviii. 326 (1954).

Table I

The chemical composition of tree leaves of different tree species at West Tofts as percentages of the oven-dry weight

Tree spp.	*Alnus incana*	*Betula alba*	*Larix leptolepis*	*Pinus nigra*	*Pseudotsuga taxifolia*
Age, years	21	21	21	21	21
% Na	0·04	0·03	0·02	0·02	0·07
% K	1·66	1·09	0·47	0·43	0·43
% Ca	2·46	1·99	1·03	0·95	1·37
% Mg	0·27	0·29	0·12	0·11	0·14
% Fe	0·021	0·014	0·028	0·013	0·014
% Mn	0·02	0·10	0·05	0·04	0·11
% SiO_2 (Insoluble residue)	0·49	0·33	1·02	0·16	0·62
% P	0·36	0·33	0·21	0·09	0·19
Total of above	5·32	4·17	2·95	1·81	2·94
% Ash	7·97	6·11	4·08	2·82	5·10
% C	51·87	55·34	57·16	60·58	60·98
% N	2·65	1·44	1·24	0·87	1·02

Table II

The chemical composition of tree leaves of different tree species at Bedgebury as percentages of the oven-dry weight

Tree spp.	*Shelterbelt (Castanea sativa)*	*Shelterbelt (Quercus)* spp.	*Quercus petraea*	*Nothofagus obliqua*	*Quercus rubra*	*Larix eurolepis*	*Thuja plicata*	*Chamaecyparis lawsoniana*	*Pinus nigra*	*Pseudotsuga taxifolia*	*Picea omorika*	*Tsuga heterophylla*	*Picea abies*
Age, years	..	..	20	21	20	22	21	20	17	20	20	22	19
% Na	0·05	0·03	0·02	0·03	0·01	0·04	0·04	0·03	0·07	0·16	0·05	0·07	0·02
% K	0·95	0·92	0·74	0·87	0·79	0·50	0·38	0·30	0·38	0·38	0·32	0·47	0·41
% Ca	0·57	0·83	0·49	0·91	0·67	0·54	1·05	1·02	0·74	0·74	0·52	0·38	0·64
% Mg	0·22	0·20	0·21	0·21	0·20	0·16	0·16	0·19	0·12	0·17	0·13	0·13	0·13
% Fe	0·013	0·015	0·011	0·016	0·008	0·018	0·013	0·014	0·013	0·015	0·010	0·013	0·011
% Mn	0·38	0·20	0·43	0·41	0·54	0·53	0·50	0·99	0·22	0·50	0·57	0·61	0·72
% SiO_2 (Insoluble residue)	0·26	0·43	0·36	0·50	0·25	0·94	0·32	0·28	0·19	0·14	0·20	0·22	0·80
% P	0·17	0·19	0·16	0·15	0·17	0·18	0·10	0·06	0·07	0·09	0·08	0·12	0·10
Total of above	2·61	2·82	2·42	3·10	2·64	2·91	2·56	2·88	1·80	2·20	1·88	2·01	2·83
% Ash	4·24	..	3·99	4·67	4·14	4·33	3·97	4·59	3·19	4·73	3·08	3·52	4·19
% C	57·13	..	56·03	57·75	58·00	59·42	63·23	62·05	63·71	61·45	62·20	59·51	63·60
% N	2·59	..	2·91	2·60	2·87	2·32	1·22	0·92	1·15	1·27	1·07	1·48	1·43

Table III

The chemical composition of tree leaves of different tree species at Abbotswood as percentages of the oven-dry weight

Tree spp.	*Quercus robur*	*Quercus* spp.	*Castanea sativa*	*Fagus sylvatica*	*Pinus sylvestris*	*Pinus nigra*	*Larix decidua*	*Picea abies* (5)	*Abies grandis*	*Picea abies* (8)
Age years	46	43	46	38	46	46	45	46	23	46
% Na	0·02	0·02	0·02	0·03	0·03	0·01	0·06	0·03	0·02	0·06
% K	1·20	1·09	1·10	0·99	0·56	0·41	0·48	0·46	0·46	0·50
% Ca	1·03	0·74	0·67	0·97	0·62	0·47	0·61	0·98	0·91	0·66
% Mg	0·22	0·14	0·29	0·19	0·09	0·10	0·17	0·11	0·16	0·09
% Fe	0·022	0·023	0·025	0·022	0·013	0·022	0·021	0·014	0·014	0·017
% Mn	0·19	0·26	0·23	0·35	0·20	0·25	0·54	0·40	0·50	0·40
% SiO_2 (Insoluble residue)	0·69	0·66	0·27	1·24	0·19	0·25	1·26	1·03	0·19	1·25
% P	0·25	0·23	0·22	0·18	0·13	0·09	0·22	0·12	0·11	0·12
Total of above	3·62	3·16	2·83	3·97	1·83	1·60	3·36	3·14	2·36	3·10
% Ash	5·63	4·84	4·86	5·69	3·29	2·87	5·13	4·49	3·88	4·38
% C	56·15	57·39	55·98	57·17	..	..	56·39	59·12	62·77	60·58
% N	2·91	2·59	2·50	2·57	..	..	2·16	1·40	1·46	1·53

THE HYBRID LARCH. *LARIX* × *EUROLEPIS* HENRY

By M. V. EDWARDS

(*Forestry Commission*)

SUMMARY

The history of the Japanese and European parents of the Dunkeld hybrid larch is surveyed fully from published records, and the descriptions of the F1 hybrid summarized. Other relevant data on *Larix* × *eurolepis* are surveyed. An experiment carried out on the progeny of the Dunkeld larch to determine its characteristics and variability is described, both in the nursery and up to the third year in the forest.

PART I. THE DUNKELD AND GLAMIS HYBRID LARCH

THE hybrid larch which originated at Dunkeld comes from seed collected from certain Japanese larch trees which are frequently cross-pollinated by European larch growing close to them.

These notes summarize the recorded history of the original Dunkeld hybrid and deal with certain of its characteristics.

As the hybrids arise from free pollination, there is no certainty that all the seed has been cross-fertilized. However, from the evidence to be quoted it will be seen that there is little doubt that the term 'hybrid' does in fact refer to hybrid plants, although this cannot be guaranteed in the case of every single individual.

THE JAPANESE PARENTS *LARIX LEPTOLEPIS* MURRAY

The first tree to yield the hybrid stands 'about 300 yards East of Dunkeld House' (Chittenden, 1932: p. 583). Seed from this tree was raised specially at the request of H. J. Elwes, probably in 1900 (see below) but in 1907 Elwes himself was uncertain if the plants were hybrid or not (Elwes and Henry, ii, p. 388).

This parent tree, together with eleven others on the 'front drive below Kennel bank' or the Avenue, as it is commonly called, about a quarter of a mile to the east of the first tree, were grown from seed brought from Japan by the 7th Duke of Atholl. This was in 1883 or 1884 (Chittenden, 1932: pp. 49, 190, and 583) and it was sown in May 1884. The twice-transplanted 3-year-old plants were put out in the spring of 1887 (Brown, 1899: p. 273). The date is sometimes given as 1885, but Brown is perfectly clear and definite that it was 1887.

In 1931 it was recorded that the eleven trees on the Avenue yielded most of the hybrid seed (Chittenden, 1932: p. 583) and this is still true. In 1899 these trees measured 18–24 feet in height (Brown, 1899) and in 1905 were almost 25 feet in height, with luxuriant foliage and some bearing cones (Murray, 1905). They had reached 50 feet by 1916 (Henry and Flood, 1919), 55 to 68 feet in 1931 (Chittenden, ibid.), and 73 to 91 feet, with a mean for the eleven trees of 81½ feet, in October 1948, after 62 seasons growth (not 64). The girth range was then 5 feet 3 inches to 7 feet 3½ inches: mean girth 6 feet 1½ inches (Matthews, 1954). Photographs of the parent of the first hybrids and of two of the Avenue trees were

published by Leven (1949). They have been described and illustrated in detail by Matthews (1954).

THE EUROPEAN PARENTS *LARIX DECIDUA* MILL. OR *L. EUROPAEA* DC

It is probable that when hybrids are obtained from the seed of the Japanese larch trees that the male parents are the larger European larch trees on Kennel bank, about 50 yards north-west of the Japanese trees and a few feet higher in elevation. Two of the finest of these trees were recorded as 180 years old in April 1931, with height 98 feet, girth 12 feet 8 inches and height 112 feet, girth 9 feet 7 inches (Chittenden, ibid.). Thus, as far as records go, they were planted about 1750, and there is a credible tradition (Atholl, 1832: p. 170) that the seed came from the original parent larches at Dunkeld Cathedral or Blair Atholl.

There are still fifteen large larches on Kennel bank, whose measurements in October 1948 ranged from 116 feet to 135½ feet in height, with a mean of 123 feet. The height and girth of the tallest (No. 11) was: height 135½ feet, girth 12 feet 10 inches. The best-formed tree (No. 6) measured 129 feet in height with a girth 10 feet 0 inches (Crawford, 1949). These trees are of exceptionally fine quality and great size, and may be claimed to be among the finest larch trees in Britain.

THE FIRST HYBRID PLANTS

'The oldest of the hybrid seedlings were planted out at Inver, near Dunkeld, in 1904, and were 25 feet high when seen in 1916, being reputed then to be sixteen years old from seed' (Henry and Flood, 1919). That implies that the seed was collected from the 1900 crop, i.e. at Elwes's suggestion. Brown (1899), however, stated that he had 'sown seed for two years, collected . . . from trees which were planted only eleven years ago'. These are the original Japanese trees from the 1884 seed, planted in 1887 (Brown was writing in the spring of 1899) and the first seed was therefore collected from the 1896 and 1897 crops and sown in the spring of 1897 and 1898. It is possible that these seedlings attracted attention in the nursery, and so prompted Elwes to suggest the special collection of 1900 and the study of the progeny to see if hybrids really had arisen.

The trees planted at Inver in 1904 are still in existence and seed is regularly collected from two of them. They were 27 to 39 feet in height in June 1919 (Henry and Flood, ibid.). One is on the bank of the stream beside the Inver sawmill and measured, in April 1953, 69 feet in height with a girth of 5 feet 6 inches at breast height. The other is beside the main road at the entrance to the Craigvinean forest houses, a few yards north of the bridge over the River Bran. This measured 62 feet tall and 4 feet 2 inches in girth at the same date. The tree beside the main road is part of a row of several, but the others are very closely confined by sycamore and other broadleaved trees, so that their girths do not exceed 4 feet and they do not yield much seed. Two other samples of the first hybrid trees were planted at Blair Atholl in 1905 (Chittenden, 1932: p. 587) and in 1949 measured 80 feet and 5 feet 5 inches girth and 78 feet and 7 feet 2 inches girth (J. D. Matthews—private communication).

Later, five hybrid trees were planted at Ladywell High Park in 1907. These

were 3 years younger from seed than the Inver trees and showed more even and better growth (Henry and Flood, ibid.). These must have been from the 1903 seed crop. None of the trees at Ladywell High Park can now be identified, and most of the wood has been felled or blown (Chittenden, ibid.).

Some of the above plants are mentioned by Murray (1905) who makes the first reference in print to the Dunkeld hybrid larch. They were inspected by the Royal Scottish Arboricultural Society in Ladywell Nursery in July 1904. However, it should perhaps be recorded that later Murray (1913) doubted their hybridity on the ground that they were too much like the Japanese parent, and that the flowering periods of the Japanese and European larches did not seem to coincide, rendering hybridization impossible. Later researches have shown that the flowering periods do in fact overlap (Laing 1944 and Leven 1951).

The Buffalo Park plot of hybrids at Murthly was planted with 300 twice-transplanted plants in the spring of 1908 (A. Murray, 1913, and J. M. Murray, 1915). These must have been from the 1904 seed crop. The first description of the hybrid is given by Murray (1915) as usually intermediate between the parents, but often of three types, one resembling the Japanese parent, one intermediate, and one resembling the European. The first type, he hinted, may be pure Japanese plants, but he had no doubt that the other two types were both hybrid. He also had no doubt about the hybrid vigour of the plants. This plot still exists, but the trees were overcrowded and are very thin and tall.

In the same year (1908) the Lower Warren wood at Dunkeld was planted (Chittenden, 1932: p. 580) and here there is now a Forestry Commission sample plot (No. S102) giving the oldest volume and yield data for the hybrids. This plot was dense in youth, and formerly included Douglas fir, so that the larch trees have somewhat small crowns.

Measurements in December 1953 were as follows: age 45 years, top height 84 feet, mean girth 39 inches, standing volume per acre, q.g.o.b., approximately 3,300 hoppus feet.

This is superior to quality class I Japanese larch and considerably superior to quality class I of European larch (Hummel and Christie, 1953), but the plot is situated on an abnormally good site.

At Glamis Castle, Angus, there was (until the gale of 1953) a mixed wood of European and Japanese larch, and in 1911 the seed collected from the Japanese trees was found to yield hybrids. A plot of these was formed, and according to information received from Mr. Crabbe, Head Forester, who was in charge of these plantations, this hybrid crop was planted in the spring of 1915 with 2-year plants. Measurements at age 29 in October 1943 were: top height 56½ feet, mean girth 20½ inches, standing volume per acre, q.g.o.b., 2,260 hoppus feet. Total crop yield to date 3,840 h. ft. (Plot No. S82). This is approximately equivalent to quality class I of European larch (Hummel and Christie, 1953).

The next description of the hybrid is that given by Henry in the *Irish Times* of 24th June 1919, which is the authority on which the specific name *Larix* × *eurolepis* is based. This was quickly followed by Rehder (1919). He stated that the plants, in the Arnold Arboretum, which were received from Dunkeld, mostly

resembled the Japanese parent, but one plant was similar in appearance to a European larch.

The classical account of the hybrid is given by Henry and Flood (1919). They differentiated it from its parents by both external and morphological characteristics of shoots and cones, and by the leaf structure, describing the hybrid as 'remarkably intermediate between the two parents' (p. 61), and stating 'All the specimens obtained from Dunkeld and Murthly seem to be uniform in their characteristics, indicating a first cross between two pure species. It is possible that some of the seed of the mother trees may not be always cross pollinated, and in that case the resulting seedlings would be identical with *L. leptolepis*; but no instance of this came under our notice' (p. 60).

The notes which follow only deal with the first generation hybrids obtained by selection of plants from Japanese (or European) larch seed. The characteristics of the progeny of hybrid larch (in the sense that the seed is collected from hybrid trees) which are of the second generation, either F2 hybrid or F1 back-crossed with either parent, is a separate matter, although often confused with the F1 cross.

PART II. A SUMMARY OF INFORMATION ON HYBRID LARCH

Seed has regularly been collected from these Japanese larches at Dunkeld and Glamis, and the resulting hybrids have been used whenever available in many parts of Great Britain. Laing's (1944) report is the most recent as well as the most detailed qualitative description of the hybrid. He describes the characteristics of both European and Japanese larch growing in Scotland and shows how much each species varies. Even among the few parents of the hybrid there are great differences in the detailed morphology of the individual trees. The hybrids obtained are probably from a number of combinations of parents. For instance, he notes that two of the eleven Japanese larch on the Avenue at Dunkeld have a special reputation for producing hybrids (see Chittenden, 1932: p. 583) and therefore there will be at least two sets of hybrids, apart from the male parent, which will vary as there are many adjacent European larches. Moreover, in some years, hybrids from some or all of the other nine Japanese trees will be included. The variations due to the different Japanese mother trees can be sorted out by separate cone collections from each tree, and such progenies are now being grown and compared by the Genetics Section at the Forestry Commission Research Station.

Laing makes clear (p. 6) the important point that the selection of Dunkeld hybrids has in the past been made on the basis of rapidity of growth. This is easily seen in the nursery, whereas morphological differences are not so obvious. In the past it was only exceptionally large plants that were considered to be hybrids, and, as is confirmed by the experiment quoted in Part III below, it is a safe assumption that such plants are true hybrids. As regards the total progeny from uncontrolled pollination, some have shoots which resemble the Japanese, some the European parent, and some are intermediate, both in shoot colour and also in other characters. Laing considers that some of these are pure Japanese larch, some hybrids resembling the Japanese parent (from which they can be

distinguished by the red or 'European' flower colour) and some are hybrids resembling the European parent. Naturally, as the seed is from Japanese trees, there can be no pure European plants.

It is desirable to investigate the progeny of the Dunkeld Japanese larch, which has been used so extensively, in more detail. The fact that, in practice, markedly tall vigorous plants can be separately recognized morphologically and by their size, and picked out to form a distinct class of hybrids, indicates that the cross may be heterotic, but to what extent has not been fully demonstrated.

It frequently happens that occasional hybrid trees are found in supposedly pure crops of European or Japanese larch raised from seed collected in many parts of Britain, not only from Dunkeld, where both species are cultivated. These are usually evident both by their greater size as well as by the different colour of their shoots, especially in winter, but the colour of the needles is also frequently obvious, especially when hybrids are found in a European larch crop. That the trees are often outstandingly large is further evidence for heterosis in some individuals, but other individuals, with the intermediate shoot or needle colour and of average size, are also found. Comparisons between *crops* of pure Japanese, pure European, and hybrid larch are, however, much more difficult to make. In the first place, the usual first generation hybrid crops are only composed of a small proportion of highly vigorous plants from a large population and these are normally compared with an average population of Japanese or European larch. This will tend to give an advantage to the hybrid crops in youth. As thinnings remove the weaker individuals from the Japanese or European crops they will include progressively larger proportions of the most vigorous trees, and may then be more closely equal in vigour to the hybrid crops. In the second place, it is not possible, under the conditions of free pollination obtaining at Dunkeld, to obtain pure seed from either the Japanese or European larch parents from which to raise comparable crops.

Recourse must be made, therefore, to the average results from sample plots of the Dunkeld and Glamis hybrid larches in comparison with sample plots of Japanese and European larch where these are growing on comparable sites. Owing to the absence of replicated plots it is not easy to be sure about the comparability of the sites, and moreover in some cases the plots compared are not of precisely the same age. However, Table I gives the results and it will be seen that in all cases except one the hybrid larch plots are taller than the Japanese, and both are taller than the European plots. Where the crops are of different age, curves (not reproduced) comparing their mean heights lie at a steeper slope than the normal growth curves for either Japanese or European larch. To what extent the rather faster growth of the hybrid plots is due to the selection of only the very tallest at the time of planting (when only the most vigorous plants were selected) or to heterosis, is at present uncertain, but it is apparently not so outstanding in older crops as in younger individuals.

Proper comparisons cannot be made without controlled pollination, and evidence of this nature is given by Langner (1951–2) who showed that the heterotic vigour of the hybrid was maintained at least up to the thirteenth year

and that volume production was then still increasing relative to either of the parents. The difference was most marked on poor sites. These comparisons were based on the tallest one-third of each of the progenies. Earlier evidence was

TABLE I. *Top heights* of hybrid, Japanese, and European larch sample plots of comparable age and site quality*

Plot No.	*Age*	*Hybrid*	*Japanese*	*European*
			Feet	
W83 . . .	26	59	..	..
W84 . . .	26	..	..	55½
S255 . . .	26	58½	..	..
S253 . . .	29	..	44½	..
S238 . . .	25	52†	..	..
S239 . . .	25	50‡	..	..
S237 . . .	25	..	48	..
S240 . . .	25	..	..	38§
S241 . . .	25	..	..	36½§
S242 . . .	25	..	..	39§
S211 . . .	23	53	..	..
S210 . . .	23	..	51½	..
E146 . . .	23	52†	..	..
E147 . . .	23	..	48	..
S195 . . .	22	50½	..	..
S201 . . .	19	..	40	..
S197 . . .	17	..	..	33
S170 . . .	20	39	..	..
S172 . . .	19	..	31½	..
S173 . . .	19	..	31½	..
S174 . . .	19	..	31½	..
S175 . . .	19	..	29½	..
S176 . . .	19	..	29½	..
S178 . . .	19	..	39½‖	..

* Top height = height of 100 trees of largest girth per acre.
† First generation hybrid.
‡ Second generation hybrid.
§ Plots of different European larch provenances.
‖ The single exception: see text.

summarized by Richens (1945), who quoted work by Pedersen, Ording, Gorsenin, and Dengler.

There is a good deal of evidence that when Japanese larch is crossed with European, the characters of the Japanese parent are dominant, both in respect of wide crown, shoot colour, and needle colour, and are also incompletely dominant

for frost susceptibility (Richens, 1945, quoting Pedersen and Albensky). The timber was investigated by Chowdhury (1931) and he showed that it resembled the Japanese more nearly than the European parent in its intimate structure. The timber was obtained from trees from Dunkeld seed. Sax (1932) showed by cytological investigations that the Dunkeld hybrid is nearer to the Japanese than to the European parent. Contradictory evidence was, however, given by Laing (1944), who reported that hybrids resemble the European rather than the Japanese parent, but details of the parents were not given. Langner (1951–2) noted that the progeny is intermediate between the parents, but differed with individual parent trees, and this probably explains the varied results.

Several workers have reported that the hybrid has a better shape, i.e. stem form and branching habit (Ording, quoted by Richens, 1945, and by Larsen, 1937, quoted below). Langner (1951–2) noted that the form of the progeny depended upon the parent tree, poor selection resulting in hybrids little or no better than the parents.

Most workers have apparently found that there is no difference between the cross *Larix leptolepis* × *Larix decidua* and the reciprocal cross, and this is substantiated by a small plot of hybrid plants from seed of European larch trees planted at Glamis in 1930. They are not distinguishable, at least macroscopically, from hybrids from the Japanese female parent. Leven (1949) gives confirmatory data. Ostenfeldt and Larsen (1930) noted that the reciprocal cross had been obtained in Denmark in 1925, but with more difficulty, and this is apparently normal, as in practice only Japanese larch seed yields hybrids freely.

Resistance to frost damage has been demonstrated as a manifestation of heterosis by some workers (e.g. Pedersen and Gorsenin, quoted by Richens), and several authors have presented evidence in favour of the theory that the cross is heterotic for disease resistance (Richens, 1945). The European larch disease or die-back is usually considered to be due to the effect of frost injury and fungal species of *Trichoscyphella* (*Dasyscypha*). The absence of susceptibility to this complex is so marked in crops of hybrid larch in Britain that it must be concluded that it is resistant. In certain Forestry Commission experiments in crops of European larch suffering from 'die-back', the survivors have been found to bear hybrid characters, e.g. in an experiment at Drumtochty forest, Kincardineshire.

Some details of the hybrids produced by uncontrolled pollination, both as regards colour, size, and form, are of value in comparison with results obtained from Dunkeld hybrid seed. A quantitative investigation of hybrid larches obtained from Japanese mother trees subject to free pollination from European trees was undertaken by Syrach Larsen (1937: pp. 92–97) in Denmark. In the spring of 1934 he sowed the seed from four separate Japanese trees in comparison with pure Japanese seed from Japan.

The progeny from two of the seed lots (S130 and S131) produced more tall slender plants than the other three. Larsen's percentage data show the largest proportion of plants from S130 and S131 in the 20–30 cm. height class, whereas in the other three progenies the largest percentages were 10–20 cm. tall. The plants were then sorted by stem colour, but at this stage as 2-year seedlings many

plants were small, and only those over 20 cm. in height were graded. The mean heights of these plants have been calculated and added in Table II and they do not differ materially for either colour or progeny. Larsen remarks 'if all light coloured plants can be considered hybrids and an increased growing energy is presumed to be connected with this fact, it is striking that the admixture of about 50 per cent. of such light plants in S133 and S134 is not seen more distinctly'.

TABLE II. *Larsen's data on Japanese and hybrid larch seedlings*

			No. of plants per height class as 2-year seedling				*Total no.*		*Mean height**
			20–30	*30–40*	*40–60*	*over 60*	*No.*	*%*	*cm.*
			cm.						
Pure Japanese		L	..	..	..	..	..	..	..
		D	247	86	29	0	362	100	29·4
Subject to cross-pollination	S134	L	52	37	6	1	96	46	30·9
		D	70	40	5	0	115	54	29·6
							211		
	S133	L	139	59	22	3	223	52	31·1
		D	178	19	7	0	204	48	26·2
							427		
	S131	L	1,171	487	123	1	1,782	97	29·5
		D	40	15	1	0	56	3	26·4
							1,838		
	S130	L	603	408	116	6	1,133	91	31·4
		D	59	29	21	0	109	9	32·5
							1,242		

L = light coloured; D = dark coloured; * Author's own calculation.

The object of this experiment had been to find out if the progeny was variable, and he concluded that this was in fact the case. But it is important to note that there was a considerable proportion of light coloured plants in the progeny of the trees subject to cross-pollination, although none in the pure Japanese progeny. These must all be considered to be hybrids, although they show no evidence of heterosis.

Larsen's photographs of the two classes of plants (his plates 3, 4, and 5) show how much better are the light-coloured plants in respect of form, i.e. straightness of stem, shoot, branching, and slenderness as opposed to bushiness.

Another quantitative investigation of the progeny of the Avenue Japanese trees at Dunkeld was carried out by Littlefield and Eliason in New York (1938).

They also found that the hybrid was of three types. They recorded the following data from 2 year 1 year transplants after five growing seasons in the forest:

TABLE III. *Littlefield and Eliason's data on hybrid larch plants*

	Japanese type	*European type*	*Intermediate*
No. of trees . . .	32	20	26
Maximum height, feet . .	10·5	13·0	13·5
Average height, feet . .	7·3	10·0	9·5

The Japanese type of hybrid which may include pure Japanese plants, was the most numerous, and the least vigorous. There was little difference between the European and intermediate types.

To sum up, it may be concluded that the Dunkeld hybrid larch is variable, both in the proportion of the plants displaying abnormal vigour, and in its colour and morphological characteristics, which lie between those of the two parents, but tend to approach nearer to the Japanese type as a rule. To what extent these results are due to an unknown proportion of pure Japanese plants in the population or to hybrids arising from different parent trees is uncertain.

Work with individual mother trees, in some cases with controlled pollination, confirms the above results to a considerable degree for *Larix* × *eurolepis* in general, but shows differences with individuals which probably accounts for the sometimes contradicting results obtained.

As existing crops of Dunkeld (or Glamis) hybrid larch of the first hybrid generation have apparently been composed only of the most vigorous portion of the total progeny, without any record of how the selection was made, it seemed desirable to examine the progeny of a normal collection of seed from the Japanese larch on the Avenue at Dunkeld, and to grow and study small samples of the whole population in the forest.

PART III. FURTHER STUDIES OF THE DUNKELD HYBRID

(*a*) *A Nursery Experiment*

In 1950 an experiment was carried out with seed of the Dunkeld Avenue Japanese larches to determine the relative proportions and sizes of their progeny (Edwards, 1952). One thousand seedlings were lifted, classified by 1-inch size classes, grouped into three distinguishable types, i.e. resembling Japanese larch, resembling European larch, and an intermediate group, and all were then lined out. The seedlings ranged from 1½ inches in height (the lower limit of the 2-inch size class) to over 7 inches. There was a small proportion of seedlings under 1½ inches but such small ones were negligible in number. After a year in the lines they were then reclassified. At this stage this is easier to do than as seedlings, and it was found best to divide each size class of the transplants into five classes, because the variation seemed continuous, and boundaries were difficult to draw. These were J = apparently pure Japanese, JH = an apparent hybrid, resembling

somewhat the Japanese larch, H = the typical hybrid, EH = an apparent hybrid, resembling somewhat the European larch, and E = apparently pure European larch.

This classification was carried out mainly on the basis of the shoot colour on 20th February 1951, at the season when the colour is most clearly defined. In doubtful cases, the position of the pulvinus was taken into consideration, as described by Henry and Flood (1919) and Laing (1944). But when dealing with many plants a little practice renders the colour classification the easiest to work on, and it is generally confirmed by the other characteristics.

TABLE IV. *Classification by size and stem type of hybrid/Japanese larch plants as 1 year 1 year transplants in the nursery*

Stem type	Size classes when lined out as 1-year seedlings, inches						Total		Mean height, inches
	2	3	4	5	6	7	No.	%	
J . . .	23	23	9	0	1	0	56	6	2·8
JH . . .	250	97	42	10	7	5	411	43	2·6
H . . .	152	161	81	55	27	4	480	50	3·3
EH . . .	10	3	1	0	0	0	14	1	2·3
E . . .	0	0	0	0	0	0	0	0	0
Totals . .	435	284	133	65	35	9	961	100	..
Per cent. . .	45	30	13	7	4	1	..	100	..

(Seed Identity No. 49/528, Wykeham Moor Heathland Nursery, Expt. 1 of 1950.)

In this sample there were no plants in the 'E' type, but in other samples such plants were found.

The data of Table IV illustrate clearly how the two types labelled 'hybrid' and 'Japanese type of hybrid' constitute the majority of the plants, irrespective of their size. From this it must be concluded that the choice of only the largest plants as hybrids, which has been the usual practice in the past and which it must be supposed was the method by which the sample plots and other crops already referred to were raised, has been a specialized method of selection which did not include a great many plants which would have been classified as hybrid on the basis of their stem colour and other morphological characteristics. Had the hybrid crops now in existence been formed of plants of hybrid appearance drawn from all size classes and not only from the most vigorous, then it is not unreasonable to suppose that their superiority to average crops of Japanese and European larch would have been even less marked that it is at present.

In the data of Table IV it is surprising to find that there is so little evidence of pure Japanese larch. Had there been two separate populations of Japanese and hybrid, the latter showing heterosis, there would have been indications of two peaks in the population curve, but this was not so. The fact that the majority of the plants were classified as H (typical hybrid) and JH (hybrid, but resembling the Japanese larch) and so few as EH (hybrid, but resembling the European parent)

shows how closely the results of this experiment approach the results of Sax on chromosomes and Chowdhury on the timber, who showed that the hybrid tended towards the Japanese rather than the European parent, as is in general true of hybrid larch crops in Britain.

The large number of intermediate type plants of small size may be noted,

TABLE V. *Percentage classification as 1-year seedlings and as 1 year 1 year transplants*

Type	*J*	*JH*	*H*	*EH*	*E*	*Total*
			%			
As first-year seedlings	53	..	45	..	2	100
As 1 year 1 year transplants	6	43		1	0	
	49		50	2		100

showing that only a low proportion of even the most typical hybrid class are markedly heterotic. This agrees with Larsen's results, quoted above.

Classification of a large range of plants showing continuous variation from one clearly marked extreme to another is always difficult, and the delimination of the classes cannot but be somewhat subjective. It is of interest, therefore, to note

TABLE VI. *Classification by size and root type of hybrid/Japanese larch plants*

Root type	*Size classes when lined out as first-year seedlings, inches*						*Total*	
	2	*3*	*4*	*5*	*6*	*7*	*No.*	*%*
J	36	15	8	0	2	0	61	7
JH	123	63	25	8	4	1	224	24
H	297	162	98	37	22	9	625	66
EH	13	4	10	3	0	1	31	3
E	1	1	0	0	0	0	2	0
Totals	470	245	141	48	28	11	943	100
Per cent.	50	26	15	5	3	1	..	100

that the results of the two classifications of the same plants, i.e. as 1+0 seedlings and again as 1+1 transplants, agreed closely, as shown in Table V.

The classification as 1+0 seedlings is much more laborious to carry out, as well as more uncertain, partly because the seedlings tend to retain their needles and the stem colour and characters cannot be easily seen, so that postponing the classification till the transplant stage is advisable.

A classification of an equal sample was also done by the colour of the root just below the collar, the method described by Laing (1944) (Table VI: compare Table IV).

Considering that the two samples were not identical, though random, the correspondence between the results by stem and by root classification is reasonably

close. The root classification is, however, much more laborious to carry out, and it requires a supply of water as the roots must often be washed to make the colour show clearly.

(*b*) *Extension into the Forest*

A random selection of the plants, classified by stem type, with no culling other than the omission of plants under 4 inches in height, was planted out in Langdale (Broxa) forest in Yorkshire in the spring of 1951. The plants were 1 year plus 1 year old. Five replications of plots containing thirty plants each were used. The mean heights of the plants were highly significantly different when they were planted, the typical hybrids being the largest, and the growth in the first season was more or less proportional (Table VII).

TABLE VII. *Early height and growth of hybrid larch in the forest*

Class of hybrid	*Height when planted*	*Mean shoot growth in first season*	*Height at 3 years of age*
	feet		
J Apparently pure Japanese . .	0·81	0·07	3·2
JH Japanese kind of hybrid . .	0·98	0·13	3·7
H Typical hybrid	1·10	0·13	3·8
EH European kind of hybrid . .	1·05	0·06	3·5
E Apparently pure European . .	0·76	0·11	3·3
Standard error of means . . .	±0·04	..	±0·16
Differences necessary for significance at levels of 5%	0·11	..	Differences not significant
Differences necessary for significance at levels of 1%	0·15	..	
Differences necessary for significance at levels of 0·1%	0·21	..	

(Broxa, Experiment No. 81.)

These figures confirm the seedling data, showing the greater vigour of the typical hybrids as compared with those resembling the Japanese or European parents.

(Note that though in this planting the numbers of plants of each class are equal, there was in fact an extremely small percentage of class E in the whole population, only about 1 per cent., and classes H and JH comprised 93 per cent. of the total.)

After 3 years' growth in the forest the plants were re-measured. Although the typical hybrids (H) are still the tallest and the extreme classes (J and E) the shortest, the differences were no longer significant. This tends to confirm the suggestion made at the time of planting out (p. 38, last par.) that the population was a homogeneous one, and not composed of two groups (pure and hybrid plants). In the absence of plants of the same parentage but undoubtedly pure origin in the experiment, no strict comparison can be made.

When these plants were planted they were classified into four groups according to the form of the plants. The regularity of the variation from J (= apparently pure Japanese) with a high percentage of good plants, to E (= apparently pure European) with a high proportion of plants with multiple or twisted leaders, or

no leaders at all, will be noted. In this experiment there was no evidence of the superior form of the typical (H) hybrid larch (Table VIII).

The differences between the form of the plants of the various classes are no longer the same, as all plants have produced a definite leader, but there is a distinction between leaders with many lateral shoots and those with few (Table IX).

TABLE VIII. *Classification of the form of the plants at planting*

Class of hybrid	*No leading shoot*	*Twisted leading shoot*	*Multiple leading shoots*	*Straight single leading shoot*
	No. of plants			
J . .	1	4	1	144
JH . .	3	1	4	142
H . .	7	3	5	135
EH . .	4	6	12	128
E . .	8	13	30	99
Total .	23	27	52	648

This distinction is of interest because in an older Japanese larch progeny trial (seed from different individual trees in Japan) one of the characteristics that has been noted is the tendency of one progeny to have leading shoots and branch leaders with many laterals, giving a pinnate branch form, and this progeny has succeeded in closing its canopy and forming a crop earlier than others. (Since this

TABLE IX. *Classification of the form of the plants 3 years old*

Class of hybrid	*Leaders without lateral shoots*	*Leaders with lateral shoots*
	No. of plants	
J . . .	13	137
JH . . .	19	131
H . . .	43	107
EH . .	61	89
E . . .	75	75

was written, these differences have been described by Schrötter, 1954.) It will be noted that in the earlier assessment (Table VIII) the J type has the greatest proportion of straight single leading shoots and the E type the least, and that the J type has now the leaders with the most lateral twigs.

CONCLUSIONS

It may be concluded that the first generation hybrid is variable in its characteristics. This is true both of its colour and morphological characteristics, its rate of growth, and its shape and form. Hybrids from the freely pollinated Japanese larch at Dunkeld and other hybrids obtained under similar conditions yield a proportion of abnormally vigorous individuals, and it is these that have been selected to form many crops of hybrid larch, but experiments also indicate that

many hybrid plants will not be any more vigorous than their parents, and this is confirmed by controlled pollination work. In most characteristics the hybrid is intermediate between the parents and usually, but not always, resembles the Japanese mother parent more than the European pollen parent. The hybrids from the reciprocal cross are apparently similar.

The value of the hybrid as a forest crop depends partly on the quality of the particular parents used to obtain the cross, and also on the proportion of the total progeny which is used to form the crop. As far as crops comprised only of the most vigorous hybrid plants (picked in the nursery stage) are concerned, there is evidence that the vigour, form, disease resistance, and hardiness of the hybrid are superior to Japanese larch and considerably superior to European larch (of the average Scottish provenance). It is not yet possible to state how much of this superiority would remain if crops comprised of plants of hybrid appearance and of all sizes were compared with similar populations of Japanese and European larch.

Considerable advances are being made in the selection and reproduction of individual trees of Japanese and European larch and these may be expected to yield hybrids of improved quality whose value will be linked with that of their parent trees.

ACKNOWLEDGEMENT

This paper is published with the permission of H.M. Forestry Commissioners.

LITERATURE REFERENCES

Atholl (1832): 'Account of the Larch Plantations on the Estate of Atholl and Dunkeld, Executed by the late John, Duke of Atholl (Drawn up from Papers and Documents, Communicated by His Grace's Trustees to the Highland Society of Scotland).' *Trans. Highland Society of Scotland*, ix. 165–219.

Brown, J. R. (1899): 'Notes on *Larix leptolepis*.' *Trans. Roy. Eng. Arbor. Soc.* iv. 271–6.

Chittenden, F. J. (1932): *Conifers in Cultivation*: the report of the Conifer Conference held by the Royal Horticultural Society. 10–12 Nov. 1931. pp. 634+84 plates. London, 1932.

Chowdhury, K. A. (1931): 'Anatomical Studies of the Wood of a Hybrid Larch.' *J. For.* xxix. 797–805.

Crawford, D. B. (1949): 'A Height and Girth Assessment of the Parents of the Dunkeld Hybrid Larch.' *J. For. Comm.* xx. 153 (circulated departmentally).

Edwards, M. V. (1952): 'Nursery Study of the Progeny of Free Pollinated Japanese Larch at Dunkeld.' *For. Comm. Report on For. Research* for the year ending March 1951, pp. 41–42.

Elwes, H. J., and Henry, A.: *Trees of Great Britain and Ireland*. 7 vols. 1906–13. Vol. ii of 1907.

Henry, A., and Flood, M. G. (1919): 'The History of the Dunkeld Hybrid Larch, *Larix eurolepis*, with Notes on Other Hybrid Conifers.' *Proc. Roy. Irish Acad.* 35 B, No. 4, 1919, 55–66, 1 pl.

Hummel, F. C., and Christie, J. (1953): 'Revised Yield Tables for Conifers in Gt. Britain.' *For. Comm., For. Rec.* No. 24.

Laing, E. V. (1944): 'Studies on the Genus *Larix* with Particular Reference to the Hybrid Larch (*Larix eurolepis* A. Henry).' *Scot. For. J.* lviii. 6–32, 2 pls., 8 figs.

Langner, W. (1951–2): 'Kreuzungsversuche mit *Larix europaea* D.C. und *L. leptolepis* Gord.' *Zeits. f. Forstgenetik und Forstpflanzenzüchtung*, i (1), 2–18, and (2), 40–56.

Larsen, C. S. (1937): 'Employment of Species, Types and Individuals in Forestry.' *Roy. Vet. and Agric. Coll. Yearbook*. Copenhagen (reprint).

Leven, J. K. (1949): 'Some experiments in cross pollination of European Larch (*L. europaea* D.C.) and Japanese Larch (*L. leptolepis* Murray). *Quart. J. For.* xliii. 57–66, 8 pls.

—— (1951): 'Flowering Times of Japanese Larch (*L. leptolepis* Murray) and European Larch (*L. europaea* D.C.).' *Scot. For.* v (2), 33–44, illus.

Littlefield, E. W., and Eliason, E. J. (1938): 'Observations on a plantation of Dunkeld Hybrid Larch.' *J. For.* xxxvi (12), 1938, 1188–92.

Matthews, J. D. (1954): 'Japanese Larches at Dunkeld, Perthshire: a Study in Variation.' *For. Comm., For. Rec.* No. 25.

Murray, A. (1905): 'Excursion to Dunkeld, Murthly and Scone, Perthshire, July, 1904.' *Trans. Roy. Scot. Arbor. Soc.* xviii. 61–64.

—— (1913): 'Notes of Silvicultural Interest.' Ibid. xxvii. 206–10 and pl.

Murray, J. M. (1915): 'The "Hybrid Larch".' Ibid. xxix, 1915, 149–56, 1 pl.

Ostenfeld, C. H., and Larsen, C. S. (1930): 'The Species of the Genus Larix and their Geographical Distribution.' *Det Kgl. Danske Videnskabernes Selskabs Biologiske Meddelelser*, ix (2). Copenhagen.

Rehder, A. (1919): 'New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum.' *J. Arn. Arbor.* i (1), 44–60.

Richens, R. H. (1945): 'Forest Tree Breeding and Genetics.' *Imp. Agric. Bureaux Joint Public.*, No. 8.

Sax, H. J. (1932): 'Chromosome Pairing in *Larix* Species.' *J. Arn. Arbor.* xiii (3), 368–73.

Schrötter, F. W. Frhr. (1954): Über zwei typen der Japanlärche (*Larix leptolepis* Gord.) in Schleswig-Holstein.' *Zeits. f. Forstgenetik u. Forstpflanzenzüchtung*, iii (2), 33–38.

AUTHOR'S FOOTNOTE

Since this paper was written, evidence of still older hybrid trees, in a plantation at La Grennach and individuals near Dunkeld Cathedral, has been found (private communications from Messrs. J. B. Hendrie and A. F. Mitchell), and this may be explained by Brown's (1899) remark, quoted above (p. 30), that he had already been sowing seed for two years.

AMENITY AND FORESTRY

(A Commentary on the Excursion of the Society of Foresters to the Lake District, 16–20 May 1955)

By T. E. EDWARDSON

(Department of Forestry, University of Oxford)

SUMMARY

An attempt is made to classify the groups of opinion likely to be opposed to commercial forestry in Britain and to identify their particular interests in the matter. The suitability of the Lake District for a demonstration to foresters of the problems arising in the reconciliation of forestry and amenity is considered, and an account is given of Lakeland forests visited, and of the subsequent discussions by the Society members of the lessons to be learned for the future. In an appendix an extract is presented of a Grizedale Working Plan for a system of management by group-selection which was frequently mentioned in the demonstrations as one of the main hopes for reducing criticism and even arousing admiration in future afforestation work.

AMENITY, in the particular sense of the pleasurable features of the countryside, presents to the British forester (be he State or estate) concerned in its creation or maintenance the complicated but stimulating problem of trying to understand and satisfy the wishes and prejudices of a number of quite distinct bodies of public opinion, while at the same time achieving what is, in most cases, his primary management aim—the provision of as constant and as profitable a supply as possible of timber and other forest products. The problem is further aggravated by the fact that the views of the interested public are frequently conflicting, and, indeed, the individual layman (or forester for that matter) may find himself possessed of a number of mutually antagonistic opinions about the part that forests should play in the country scene and in rural activities.

It is safe to assume from the great deal that has been written in the press, particularly in the last two or three decades about the activities of the Forestry Commission, that the prime objection of all forestry opposition in this country is to the establishment for commercial working of extensive, monotonous exotic conifer plantations—the 'goose-stepping monocultures' so hated and harried by the journalistic snipers. It is likewise clear that this combined volume of objection is built up from at least four separate contributing sources whose interests and motives it is profitable for the forester to study and whose identities for discussion can conveniently be designated as first the local resident, second the urban country-lover, thirdly the field naturalist, and lastly the local trader including farmers.

The most sensitive, and yet in some ways the most aware of the forester's frequent dilemma, is the country dweller of long standing with his quite simple, uncommercial desire that his neighbourhood and its landmarks should remain much as they have been throughout his lifetime, cherished links with childhood

and other 'days gone by'. Doughty champions of a forestless *status quo* for Exmoor or Cheviots find themselves here in contrary company with guardians of trees, ancient and ornamental, from Burnham Beeches to the Black Wood of Rannoch. Here too must go at least one illustrious forester, inheritor of mature Tronçais-class oak, who yet finds, unabashed, specious reasons for 'letting the Copse go on a little longer' to grace the vale of Wye.

In *Innisfree* Yeats speaks the pavement thoughts of a second group of opposing voices, the city-bound country-lovers, great in numbers, but, as a body, more erratic, more catholic and in some detail less critical in interest than the last. These ramblers, climbers, picnickers, week-end motorists, artists, and the like look to the countryside, in their brief forrays, for all that is anti-urban, a place of recreation, a colourful, attractive but passive background for their temporary change of occupation. For many in this large and intellectually amorphous company the distant broad pattern of hill and wood is almost all-sufficient: for them there is scarcely in a sense any middle ground, their knowledge of scenic detail and their interest in it extending little beyond, at worst, the motor roads and, at best, the access paths.

The forester finds in a third group many kindred spirits, for they, like him, are the active field naturalists, be they observers and collectors of flowers, insects, or birds, or sportsmen intent on fish, fox, or game. All of them look to the country's woods and open ground to protect and provide the living objects of their immediate interest.

The rural traders, attuned in the course of business to the current trend in the wishes and opinions of the 'visitors', and generally prepared to press their views in local council with the object of ensuring a profitable flow of trade with a minimum of apparent commercialization, make up, along with the forest-competing commercial land-using interest, the farming community, the fourth important body of opinion which the forester finds in a state of potential or active opposition to his operations, and which he must study and, if he can, convince of his beneficial intentions.

There can be little point in questioning the desirability of such powerful and critical appraisal of the forester's handwork: he is, after all, in the exciting and responsible position of being able in a few brief years to mark and alter both the detail and the broad canvas of the landscape for what may well be two or three centuries to come. It was the realization of the importance and topicality of this problem for many of its members that led the Society of Foresters of Great Britain to frame the 1955 Annual Excursion around the subject of 'Amenity and Forestry' and to set as the aim of the week's demonstrations and discussion the reconciliation of commercial forestry undertakings with general rural amenity.

Several parts of Britain suggest themselves for the field study of such a topic, but no single one save the West Highlands combines as does the area selected—the Lake District—the long-established reputation for a varied attractiveness of much-publicized lake and fell and 'natural' scrub woodland, the close proximity to large industrial areas from which visitors come year after year, and a local community largely dependent on either the tourist trade or farming, and in particular

sheep farming. Added to this is the attraction that every forest-promoting interest in Britain is compactly represented, from the straightforward commercial timber production-with-amenity of the Forestry Commission and private owner to the amenity-with-timber production of the National Trust and water conservation-with-timber of a city corporation.

In the Lake District criticism of afforestation is not new: among others, William Green, the artist, expressed his elegant disdain of the 'tasteless spriggery' of larch and beech planted on the Isthmus at Derwent Water more than one hundred years before the Acland Report. The critics of the day showed no aesthetic discrimination: condemned alike were the commercial plantings of Derwent's Great Wood and the amenity planting of Friar's Crag and Lord's Island. Seeing these woods today, the forester is entitled to take heart for the task ahead from the contribution they make to the present beauty of Derwent Water (Plate II, Fig. 1).

Despite this evidence, the opposition to the Forestry Commission's work begun in 1920 in the Lakes was such that by 1935 it was decided to set up a Joint Informal Committee of the Forestry Commission and the Council for the Preservation of Rural England to consider how the interests of timber production and amenity, where divergent, could be reconciled (1). The Committee recognized that large-scale afforestation and the preservation of areas of natural beauty were both necessary on national grounds, and that the land available for both purposes was limited; the solution to the problem they considered could only be co-operation or at least a just correlation wherever otherwise the two would conflict. The outcome of their deliberations was that 300 square miles in the central part of the Lakes were reserved from State afforestation and a further block between Windermere and Devoke Water was made subject to special attention to amenity, including the use of broadleaved trees and care in the layout of forest rides. In 1954 changed economic conditions affecting the maintenance of private woodlands in the central block led to the Committee agreeing to Forestry Commission acquisition in the reserved area provided restocking with hardwoods was the primary objective.

The Society's excursions this year included woodlands both within and without the 1935 reserved area. On Derwent Water, inside the area, visits were paid to Lord Rochdale's Home Woods at Lingholm, and to the National Trust's Manesty Wood. Also within the block, the Society saw some of the woodlands on Lake Thirlmere of the Manchester Corporation.

Of the Forestry Commission's forests, lying outside the central area, Thornthwaite (2), the earliest Commission project in the Lake District, and Grizedale, stretching between Coniston and Esthwaite Waters, were visited.

Each area added its share to the presentation of the general problem. Thornthwaite, lying fully and steeply displayed to critical inspection in the laps of Skiddaw and Grisedale Pike, on soils once considered too poor in general for species other than conifers and showing in plantation pattern and ride layout the prentice hand of early Commission years (Plate II, Fig. 2), was an obvious target for one group at least of those rural 'Friends', described recently by J. D. U. Ward (3)

L. & M. Gayton

FIG. 1. Wooded landscape on Derwentwater. Great Wood larch in the right foreground. In the background Dodd Law between Skiddaw and Lake Bassenthwaite

J. Hardman

FIG. 2. Plantations dating from 1929 and 1930 on Dodd Law in winter. Pines and spruce at the high levels, larch on the middle slopes and douglas fir at the hillfoot

PLATE II

J. Hardman

FIG. 3. Mixed, mature conifer forest at Tarn Hows. Plantations, once resented, but now generally accepted as beautiful

R. S. Troup

FIG. 4. A *femelschlag* regeneration group, chiefly beech, in a forest of spruce, beech, and silver fir of high commercial value at the Forest of Bienne, Switzerland

PLATE III

as partisan 'Enemies of Forestry' under a more appealing banner. Grizedale's oak woods, by contrast, lying on richer soils in more rolling country, offered tempting prospects of intensive management for a sustained yield in harmonious combination with scenic demands.

At Thirlmere there was evidence of a pendulum swing from early group-wise plantings, combining amenity with water catchment and timber production, to later afforestations where groups seemed much less obvious, and latterly a swing back again to an interest in group working and the clearing of views between road and lake. On the National Trust property emphasis was again somewhat different; here was a case of the woodlands having established themselves with age as an adornment of the scene and the problem of acknowledging their maturity and taking steps to regenerate with minimum disturbance to the general character of the woods. And finally at Lingholm discussion was concerned with micro-amenity, amenity at close quarters, the appeal of the colour and form of the individual trees rather than the overall appearance of the wood at a distance: again the need for gradual, inconspicuous, irregular working to retain character was emphasized.

With those demonstrations of the varied aspects of the amenity problem fresh in mind, the differing opinions of the Society's members, unfolded and debated piecemeal in the woods, were given a chance at the customary technical discussion on the last evening of acquiring some coherence within a framework, tacitly established and agreed, of basic principles of naturalness, gradualness, and reasonableness in the application of the forester's art.

Naturalness, in this context, had no ecological significance: it was an assessment of what the public appeared to appreciate in the woodlands, and the Dodd Wood at Thornthwaite was in all respects the chastening antithesis—hard lines between wood and fell, geometrical planting blocks, pure in species, glaring in contrast, and vast in extent, the whole, for good measure, broken up by a hill-long series of conspicuous vertical rides. Of interest, obviously, were the reasons, apart from the unavoidable selection of conifers on most sites, for departure from a more generally acceptable woodland pattern—the need to fence against sheep, the early pressure to plant every fenced acre, the assumed technical simplicity of dealing with pure blocks, and the uncertainty regarding the eventual mode of extraction on steep ground. Significantly, the planting of trees in straight lines, that other frequent lay objection to 'regimented conifers', caused no anxious heart-searchings in discussion. Effective comparison was made here with the necessary use of scaffolding in the creation of architectural beauty; following thinning and the development of form and character with age in the individual trees (Plate III, Fig. 3), the straight planting lines would certainly disappear, as also would the 'monotony' so commonly claimed for young conifers, and shared (as a normal infliction of adolescence) even by young hardwoods in pure crop.

What, then, on Dodd Law were the real causes for concern, the important lessons to be grasped for the improvement of future effort? For a few diehards there were none; here for one such was an example of the forester attaining his objective on a suitably grand scale with the minimum of technical complication.

Or, from a more fundamental viewpoint, justification was sought by another through criticism of what was being accepted as all-sufficient for amenity. Surely, he claimed, there was more to it than the mere emotional satisfaction to be got from the lively and deliberate variation of sylvan colour and form: should we not as foresters hesitate before complicating management merely to gladden the eye; was not our true policy rather to educate the public to acquire the intellectual satisfaction of a real appreciation of the place of a forestry enterprise, untrammeled by complicating adornment, in the pattern of rural land-use?

But, for the majority, the lessons seemed clear: the general indications were that vertical rides had no longer the justification of providing effective fire-breaks or lines of extraction, and, in areas of high amenity value at least, they should give way to more useful and much less obvious contour roads. The planting pattern again was capable of diversity with little additional complication in management: mixed stands, in particular of hardwoods and conifers and varying in age, offered the best prospect of success with the public, but, as a second best, small pure stands of irregular shape would go much of the way to remove antagonism. Thirdly, the junction of wood and fell must be softened, preferably by controlling sheep to the extent of making plantation fences unnecessary, or, should fences be required (and here there is no easy compromise to be found between forester and farmer), irregular patches of ground close to the fences must remain unplanted.

Lastly, in the search for a more natural-looking forest, the forester must be prepared to accept within the plantations, and in particular along roadsides, uneconomic but attractive areas of hardwood scrub.

Gradualness as the second guiding principle meant, in practice, accepting the fact that any change, if sufficiently brutal and obvious, would meet with resistance. In the creation of the large new forests criticism on this score had been unavoidable, but for the future, with an adequate forest estate in being, the process of change and regeneration should be modestly veiled within the forest and helped in this direction by 'irregular' group-selection working on the lines of the Swiss *femelschlag* (Plate III, Fig. 4). A pleasant prospect for the future, but one to be attained only after dealing effectively with the difficult problem of hill sheep encroachment within the forest and the consequent need for uneconomic quantities of wire in irregular working. A prospect, too, not uncomplicated by the effort of management and supply of labour needed to maintain a 'planned disorder' (4). In the appendix to this paper, as an example, are extracts from the Forestry Commission's Grizedale Forest Working Plan for the group selection management of the Hardwood Working Circle visited by the Society.

What, in following his third guiding line, is required of the forester in the way of reasonableness beyond the inevitable give and take in his future dealings with the hill sheep farmer? The answer for many members was a fuller appreciation of the public viewpoint: change is inevitable and with it go changes in accepted standards. Unlike the public, most foresters have had the opportunity on the Continent and elsewhere of seeing examples of successful combinations of commercial forest management with great natural beauty. The immediate task then

should be the education of the public in silvicultural matters towards the time, shall we say a century hence, when, in a countryside adorned with commercially valuable woods and forests of mixed broadleaves and conifers and of irregular structure, the local resident, so far as forestry is concerned, is conditioned to the constancy of modest change, the country-lover is charmed to silence by the variety and form of both distant vista and the forest's serene depths, the naturalist is embarrassed by a wealth of 'objets de chasse', and the traders and farmers recognize in the forester a fellow trader with an eye at least equal to their own for the beauty of the countryside in which he lives?

ACKNOWLEDGEMENTS

The appended extract is published with the permission of the Conservator, Forestry Commission, for North-West England. The Lakeland photographs are selections from suggestions made by H. L. Edlin, Esq., Forestry Commission. The illustration of Swiss *femelschlag* at Bienne is from a photograph by the late Professor R. S. Troup, which was kindly lent by the Imperial Forestry Institute.

LITERATURE REFERENCES

(1) Joint Informal Committee of the Forestry Commission and the Council for the Preservation of Rural England: *Agreements on Afforestation in the Lake District.* A report published by H.M.S.O. (1955).
(2) Forestry Commission: *Britain's Forests: Thornthwaite.* H.M.S.O. (1951).
(3) Ward, J. D. U.: 'Forestry and People.' *Quarterly Journal of Forestry*, xlix. 3 (1955).
(4) Anderson, Professor M. L.: Manuscript Working Plan for Bagley Wood, Oxford (1951).

APPENDIX

Summarized Extracts from the Working Plan for the Hardwood Working Circle of Grizedale Forest for the period Oct. 1953 to Sept. 1965

Introductory Note. The plan was prepared by Mr. J. V. Crosland, District Officer, revised and amended by Mr. J. R. S. Chard, State Forest Officer, and approved by Mr. C. A. J. Barrington, Conservator, Forestry Commission. It is in two parts, which accord with conventional Working Plan presentation except that Part I, Chapter III, is prescriptive.

PART I

Chapter I. General Description of the Area (summary)

The plan area is 516 acres and comprises oakwoods lying in the Grizedale valley in an irregular band between the major conifer crops on the higher hillsides and the permanent agricultural ground in the valley bottom.

Rabbits and hares have hitherto been easily controlled, red, fallow, and roe deer cause sporadic damage, particularly the roe. Sheep have caused considerable damage in the past, but improved fence erection and maintenance have reduced the damage.

Chapter II. Former History and Utilization of Hardwood Crops (summary)

Woods managed until about 1900 as coppice with standards for local industries—coopery, tanning, charcoal burning, iron smelting, swill making, and bobbin turning. When heavy

iron smelting demands ended, the value of the woods fell and sheep grazing was introduced as alternative rental. This stopped natural regeneration, weakened the oak stools and degraded the soil: the grazing misuse is responsible for the present poor crop condition.

Chapter III. Division and Allotment of Areas (summary)

One Hardwood Working Circle proposed, divided into six equal blocks, made up of sections totalling forty-nine for the Circle. The Plan period is twelve years.

Chapter IV. Section Descriptions and Past Treatment Records

A typical section description is that for Carron Block—Sections 1, 2, and 3—65·3 acres. 'The main species is a pure form of sessile oak. The crop was last cut over for coppice 60 years ago and was last thinned about 1910. In general the form of the oak is good, but the age of the stools and the lack of regular thinning has resulted in very restricted crowns. Other hardwoods include scattered groups of alder and sycamore, with a few poorly developed ash. The sycamore shows some promise. There are some prime quality European larch about 100 years old scattered over the area. Some in Section 3 are to be used as a seed orchard.'

PART II

Chapter I. Management and Yield (summary)

Objects of management

1. To perpetuate the existing hardwood and mixed woodlands in the Grizedale valley as predominantly hardwood high forest (*a*) to supply produce for existing and potential local industries and crafts, dependent on hardwoods for raw material, (*b*) to maintain and enhance the amenities of the Grizedale valley.

2. To convert the existing coppice and clear felling system of management to uneven aged selection forest, propagated ultimately by natural regeneration from seed.

3. To improve the quality of the growing stock, and to achieve and sustain the maximum volume production consistent with this aim.

4. To test new species of hardwoods, and in particular *Nothofagus* spp., over the poorer sites, while maintaining the largest practicable proportion of indigenous oak on those sites best suited to its development.

5. To regenerate naturally from the best strains of the older Grizedale larch, and to grow a scattering of selected stems of this species to boat-skin quality.

6. To study the economics of growing and managing hardwoods under the selection system in the Lake District soil and climate and to provide a demonstration of the methods employed.

Choice of species (summary)

Future choice will be directed to favouring the existing species—sessile oak, birch, alder, sycamore, European larch, ash, and wych elm.

Silvicultural system

The crops will be treated under a group selection system, by which it is understood that there will be no extensive clear felling and that the canopy will be opened for regeneration just sufficiently to ensure establishment of the species desired: in one operation in the case of light demanders and progressively, following advanced growth, in the case of shade bearers. Thereafter the groups may be enlarged concentrically but should not normally exceed an acre or so in extent. Initially, groups will be established by the artificial restocking

of blanks and the progressive replacement of patches of inferior growth in the existing, generally even-aged, crops. Cleanings, thinnings, and improvement fellings will be carried out simultaneously with seeding and regeneration fellings, covering the whole area of the working circle on a regular cycle. The cycle proposed is 6 years, and normally one Block will be treated each year.

Rotation (summary)

No fixed rotation. All species will be grown to a maximum size subject to the maintenance of satisfactory increment either by volume or quality, and the requirements of regeneration.

Determination of the yield (summary)

It is proposed to regulate the yield under the *méthode du controle* or standing check method, separately for each Block as follows:

1. All trees over 6 inches q.g.b.h. to be enumerated every 6 years in each Block prior to treatment. Each tree recorded to be scribe-marked at point of girthing.

2. From the enumeration, using species tariff tables, the initial standing volume (*SI*) in each Block by species and size groups will be compiled, the volumes to be recorded as tariff feet (*T* feet).

3. All trees over 6 inches removed in thinning and regeneration work (generally immediately after enumeration) to be measured both standing and felled and booked for tariff volume as for the initial standing volume. The tariff volume of those removals is designated as the periodic yield (Ya).

4. Standing and felled measurements will likewise be kept for accidental or additional fellings during the 6 years, the tariff volume being designated as interim yield (Yb).

5 and 6. At the next enumeration, all trees will be girthed at the previous mark and recruited trees, now 6 inches or over, will be scribed as before. From this will be got a fresh estimate of the standing volume, designated as the subsequent standing volume (*SII*), which will include the trees recruited in the period, designated as recruitment (*R*).

7. Increment in tariff feet is then derived as follows:

$$\text{Increment} = (SII + Y(a+b) - R) - SI.$$

This Block increment will be analysed by species and size groups.

8. Yield. The prescription of yield, based on the assessment and analysis of increment during the previous cycle, will be made before each periodic felling is marked and will state in broad terms the approximate number of trees over 6 inches q.g.b.h. by principal species and size groups (and where necessary by Sections) which are considered due for harvesting. This will be a guide only to those marking and may be modified by silvicultural requirements; in this connexion it is emphasized that within reasonable limits the effects of control are intended to be cumulative and progressive and that anything which cannot be achieved in one operation will still be capable of adjustment in future cycles. The volume estimates coupled with these prescriptions will be applied as a general check against the total yield, by size groups only, for the Block as a whole; this will be done after marking and it should be remembered that the figures are in 'tariff', not Hoppus feet. No yield is prescribed for trees of 6 inches and under in q.g.b.h., the marking of which will be dictated solely by silvicultural considerations.

9. The tariff tables for each principal species will be prepared and revised from time to time on the basis of the measured volumes of the trees of the periodic yield. The eventual aim is separate tariffs for each principal species and Block.

Chapter II. Prescriptions (summary)

In the first 12 years (two enumerations) the principal tasks will be (*a*) complete restocking

by planting or otherwise of blanks; (*b*) rehabilitation or enrichment of all devastated or derelict areas; (*c*) systematic cleaning, thinning, and improvement fellings in existing crops; (*d*) conservation of increment pending assessment of the potential sustained yield; (*e*) to initiate trials of new species; (*f*) to develop local markets; (*g*) to test and improve the methods of management proposed and to gain maximum insight of the silvicultural problems ahead. To save time two Blocks per year will be worked through in the first 12 years, but only one will be enumerated each year. Special prescriptions include experimental investigation in a small area of each Block of natural regeneration of the indigenous oak, since there is little knowledge or experience of the silvicultural needs for hardwood seeding and regeneration fellings in the Lake District.

Chapter III. Plans of Work F.Y. 54 to F.Y. 65 (summary)

These tabular plans comprise (A) areas for restocking, (B) order of enumeration, and (C) areas for oak regeneration trials.

Chapter IV. Records and Control (summary)

Maintenance of plan records and amendments, record forms, and the revision of the plan.

GROWTH STIMULATION OF FOREST TREE SEEDLINGS BY THE ACTIVITY OF FREE-LIVING MYCORRHIZAL MYCELIA

By IDA LEVISOHN

(*Bedford College, University of London*)

SUMMARY

Observations by the late Dr. M. C. Rayner on a field experiment and the results of subsequent pot-culture experiments demonstrate that the soil activity of mycorrhizal fungi can improve the development of forest tree seedlings (*Picea*, *Pinus*, *Betula*) before actual mycorrhizal infection takes place. Further experiments show that ectotrophic mycelia are capable of stimulating endotrophic tree species (*Fraxinus excelsior*, *Chamæcyparis lawsoniana*, *Robinia pseudacacia*), i.e. that these ectotrophic mycorrhiza-formers bring about growth stimulation of the plant although no infection is formed at a later stage. It is suggested provisionally that at least some ectotrophic mycelia, *Boletus scaber* and *Rhizopogon luteolus*, may influence seedling growth by attacking soil organic matter and liberating 'nutrients' from which the higher plant benefits.

INTRODUCTION

BASED on the findings of the Wisconsin researches, Wilde, in a paper to the 8th International Botanical Congress (10) and in a recent publication in *Soil Science* (11), discusses certain aspects of the soil life of mycorrhizal mycelia and stresses the role of their rhizosphere activity in tree development. Although research workers seem to agree that the presence of mycorrhizal fungi in the soil can favour the growth of the higher plant, no experimental evidence has been available so far to show that mycorrhizal mycelia *per se* are capable of improving tree growth.

Wilde (10, 11) who attributes the arrested growth of trees in Wisconsin grassland soils to the absence of mycorrhizal fungi observes 'that seedlings raised in forest soils continued to grow satisfactorily in prairie soils even though their root systems lacked mycorrhizal short roots or internal mycelia'. He maintains 'that development of ectotrophic or endotrophic mycorrhizae in trees is only one incidental detail of a broader relationship of the rhizospheric symbiosis'. However, the result of these particular Wisconsin experiments with plants introduced from forest soil into nursery soil is no incontrovertible proof that mycorrhizal mycelia are the agents responsible for the satisfactory growth in the prairie soil. Since transplanting necessarily involves soil inoculation, there is reason to argue that organisms other than mycorrhizal fungi might be the cause of processes leading to the good growth observed.

Burges (1) expressed the opinion that in the nutrition of the higher plant the infection itself is of no consequence, but that the activity of the free-living mycelia might be of decisive importance. Observations on field and pot-culture experiments in which conifer seedlings were treated with mycorrhizal inocula, led Rayner (7) to the view that the stimulus to plant growth is frequently antecedent

to mycorrhiza formation, in other words that apart from effects due to the actual invasion of the root tissues by mycorrhizal mycelia, there must be present in the soil an external activity of the mycorrhizal organism capable of influencing tree growth. Levisohn (3, 4) described experiments the results of which demonstrate that mycorrhizal fungi, without forming associations with the roots, can improve seedling development.

The following communication is concerned with further studies on the effects produced by rhizosphere activity of mycorrhizal mycelia on the growth of forest tree seedlings before or without an actual fungal invasion of the root tissues taking place. (The term 'rhizosphere' is used here in a general sense and applies to the whole ball of soil around the root.) Included in this paper are unpublished observations by the late Dr. M. C. Rayner on a particular field experiment.

RAYNER'S OBSERVATIONS ON AN INOCULATION EXPERIMENT IN THE FIELD

Among the successful cases of fungus inoculations carried out by Rayner was an experiment designed to introduce the mycelium of *Rhizopogon luteolus* in a research nursery at Wareham, Dorset. In 1945, at the time when the experiment was conducted, *Rh. luteolus*, though growing in plantations in the vicinity, had not invaded the nursery. *Boletus bovinus*, present all over the Wareham area, was the only fungus observed to form mycorrhizas with the pine and spruce species raised within the nursery.

It had been demonstrated that, under the conditions existing in the nursery and the routine cultural methods applied, *B. bovinus* failed to produce mycorrhizal infection in Sitka spruce during the first year of growth. Therefore it was considered desirable to introduce the mycelium of a fungus that might establish mycorrhizal contact at an earlier stage of development. With this end in view, bed 27 (Plate IV, Figs. 1 and 2) of a certain section in the nursery received inoculation with sporophores of *Rhizopogon luteolus* in the autumn of 1943 and 1944 during which years the bed was also supplied with the standard compost dressings. In the subsequent year, 1945, Sitka spruce was raised without either compost treatment or sporophore inoculation. The seedlings showed good growth which was ascribed to the possible residual effect of the compost plus the result of fungus inoculation. Microscopic examination carried out during the autumn revealed that the very well-developed root systems of the seedlings had mycorrhizas unlike the type usually found in the nursery for which the mycelium of *Boletus bovinus* had been found responsible. It was inferred that the new type of association was formed by *Rhizopogon luteolus* although no isolations were made at the time. This inference received support later by the isolation of *Rh. luteolus* from the characteristic infections exhibiting a rather large mantle of pale yellow colour.

The experiment, taken by itself, would only have demonstrated the early formation of mycorrhizas by *Rh. luteolus* and its possible effect on seedling growth but for the circumstance that the next door bed, 26 (Fig. 2), showed an unexpected behaviour. This bed, separated from the inoculated bed by a path 1 foot wide, had also been sown with Sitka spruce in 1945, but treated as a control bed

FIG. 1. Spread of stimulus to growth of Sitka spruce seedlings caused by the rhizosphere activity of *Rhizopogon luteolus*. Sugar Hill Nursery, Wareham, Dorset, section 3, bed 27 (left) having received incolulation with sporophores of *Rb. luteolus* in addition to compost treatment; bed 26 (right) without fungus inoculation or compost treatment. Photograph early November 1945

27	COMPOSTED 1943, 1944 × RH. LUTEOLUS
26	NO COMPOST NO INOCULATION
25	COMPOSTED 1945 NO INOCULATION

FIG. 2. Condition of Seedbeds, 1945

PLATE IV

FIG. 3. Seedlings of Lawson cypress in their second year of growth: (A) Control. Soil not inoculated; (1 A) Soil inoculated with pine mycorrhizas formed by *Rb. luteolus*; (2 A) Soil inoculated with non-mycorrhizal pine roots

FIG. 4. Seedlings of *Robinia pseudacacia* L. 4 months from sowing. Top series: sterilized soil, not inoculated. Bottom series: sterilized soil inoculated with *Boletus scaber*

PLATE V

receiving neither compost nor inoculations. At the end of August the seedlings of the control bed showed the usual poor growth except at the side adjacent to bed 27 where better seedlings developed. On the other hand, the control bed exhibited no stimulated growth on the side nearest to bed 25 (Fig. 2) which had been composted in 1944 and 1945 and carried an excellent crop of Sitka and Norway spruce (which were not mycorrhizal).

The first impression was that the improved development of the Sitka seedlings along the one margin of bed 26 represented the well-known phenomenon of the edge effect frequently recorded in nursery beds, in particular on relatively 'new' soil. This impression, however, was soon revised when it was observed that the stimulus to growth spread gradually throughout the whole bed. Fig. 1 shows the condition in early November 1945. The behaviour of the seedlings pointed to the invasion of the control bed by the mycelium of *Rhizopogon luteolus* from the neighbouring bed. This interpretation received strong support from microscopic study of the roots. Systematic examination showed that in September the stimulated plants had well-developed root systems with a conspicuous 'mix-up' of root hairs and rhizomorphs of *Rh. luteolus*. At this stage, no trace of mycorrhizal infection was detected. It was therefore concluded that the stimulation of the seedlings in the control bed was caused by the external activity of the mycelium of *Rh. luteolus* before an actual invasion of the root tissues had taken place. From November onwards, mycorrhizal associations of the same type as those occurring in the inoculated bed 27 were recorded. Seedlings from the side of the control bed proximal to bed 25 continued to show poor growth during the year. Their defective root systems with a scanty supply of short roots were found to be non-mycorrhizal.

Following the observation on the spread of stimulus to growth of Sitka spruce, similar instances were recorded for *Pinus nigra* demonstrating that the soil activity of *Rhizopogon luteolus* is capable of favouring the development of coniferous seedlings other than Sitka spruce.

POT-CULTURE EXPERIMENTS

Experimental details

The experiments were carried out in the very poor heathland soil from the Wareham area (7) in which, except for *Boletus bovinus*, ectotrophic mycorrhiza-formers were absent. This soil had also been observed to be free from mycorrhizal associates of *Sequoia*, *Thuya*, cypresses, and other endotrophic tree species. Untreated soil was used in preference to partially sterilized soil for the following reasons: (*a*) sterilized soil produced relatively good seedlings thus not allowing for a full demonstration of the growth response to the inoculum; (*b*) the activity of the inoculated mycelia proved to be more vigorous in the unsterilized soil employed in the experiments.

Mycorrhizal inocula were applied to the soil before sowing in the form of infected root fragments superficially sterilized with mercuric chloride or as pure culture mycelia. In the latter case, controls received an inoculum of culture

medium equal to that introduced with the mycorrhizal fungus from pure culture. In the pot-experiments in which infected root material was inoculated, control cultures were supplied with sterilized roots or with uninfected roots especially raised for the purpose. The amount of inoculating material per pot was equivalent to 0·5 g. dry root material.

The experimental plants were grown in a Möller house for at least 2 years and then transferred to gravel pits nearby.

Diagnosis of the soil activity of mycorrhizal fungi as reflected in the growth stimulation of the higher plant is not easy. In nature, it is often only by chance that one catches the 'critical phase' i.e. the period of non-infection between the observed improvement in growth and the onset of mycorrhiza formation. During the experimental studies in pot-cultures, greatest care was taken as regards root examination which was carried out by sectioning at frequent intervals. In some of the pot experiments, fortnightly examinations were made regularly for 2 years.

Effect of specific mycorrhizal mycelia

Root inoculation. Increased growth of various pine species before mycorrhizal infection had taken place was observed following the introduction of active mycorrhizas in the potting medium. The inoculum, root fragments of Scots pine infected by *Rhizopogon luteolus*, was particularly effective in the case of *Pinus contorta* which reflected the external fungal activity as early as 4 months from sowing (and inoculation).

Among endotrophic species thus treated, ash (*Fraxinus excelsior* L.) showed considerable benefit—long before an association was established—by the soil activity of the endotrophic mycelium introduced in the form of mycorrhizal ash roots. Four months after sowing, 80 per cent. of the controls had died and the few survivors were extremely poor, while for the inoculated cultures growing in the same heathland soil of pH about 4 and very deficient in nutrients, growth stimulation was recorded. There were no losses in the inoculated series and the plants improved steadily in height and colour. Not before the end of the second growing season was mycorrhizal infection observed in some few seedlings of the inoculated cultures.

Pure culture inoculation. In most cases in which inoculation with mycelium from pure culture was applied, the results of the experiments were disappointing. It would appear that this is due to the physiological condition of the mycorrhizal fungi in pure culture. Among the number of mycorrhizal mycelia tested, *Boletus scaber*, a well-known associate of birch (6), proved an exception. When the fungus was introduced in birch cultures, growth of the plants was found to be favourably affected by the activity of the free-living mycelium. In these experiments seedlings of *Betula verrucosa* were grown in composted Wareham soil since poor and irregular germination of the birch seeds had been observed in the untreated soil. From the later part of the first growing season onwards, the seedlings of the inoculated cultures started to exhibit increase in shoot length, improvement in colour of foliage, and enlargement of leaf area.

By way of example may be cited the figures for measurements of the leaf areas

of three average plants from both the inoculated and the control series. At this stage, no mycorrhizal contact had been established.

Leaf areas in cm.² of seedlings inoculated with B. scaber (*A*+, *B*+, *C*+) *and control seedlings not inoculated* (*A*, *B*, *C*) *recorded from the apex downwards*

A+	*B*+	*C*+	*A*	*B*	*C*
51·0	48·2	39·0	18·8	15·8	10·1
46·9	37·2	38·8	22·8	16·9	11·0
35·4	22·1	35·0	24·8	18·0	14·2
32·1	20·0	21·6	22·6	17·2	18·1
21·4	20·0	16·1	..	17·3	..
25·7	22·2	17·7	..	..	..
25·7	25·6	14·8	..	..	..
27·1	27·0	..	..	..	..
23·3	..	..	..	..	..
29·0	..	..	..	..	..
			average		
31·76	27·75	26·18	22·25	21·3	13·35

Measurements were made with a planimeter of the areas of the leaves still remaining on the current year's axis on 16th September 1953. The leaf at the extreme apex was not recorded since growth for the season had finished before it had had time to reach its full size; with this exception, the figures represent the areas of the leaves from the apex downwards in each plant. (Note tendency in inoculated series (A+, B+, C+) to show larger leaves at the close of the growing season, whereas the tendency shown by plants A, B, C is rather the reverse.)

Effect of non-specific mycorrhizal mycelia

It is very difficult to ascertain with absolute certainty that in a given root system no trace of mycorrhizal infection is present. Here, as in many other instances, the negative evidence, although it may be highly suggestive, often leaves the research worker vaguely dissatisfied. In order to eliminate all chances of overlooking the presence of an infection induced by the experimental mycelium, inoculation experiments were carried out using ectotrophic mycelia for endotrophic tree species and, vice versa, endotrophic mycorrhiza-formers for ectotrophic plants.

The results of introducing root fragments of Scots pine (*Pinus sylvestris* L.) infected by *Rhizopogon luteolus* into cultures of Lawson cypress (belonging to the endotrophic type of tree) have been recorded elsewhere (3, 4). It was demonstrated (Plate V, Fig. 3) that the Lawson seedlings showed pronounced benefit by the activity of the free-living ectotrophic fungus which was not able to establish mycorrhizal contact with the roots. Likewise *Thuya plicata*, also an endotrophic species, showed definite growth stimulation following the inoculation of *Rhizopogon luteolus* mycorrhizas.

Boletus scaber introduced as pure culture mycelium was found to improve growth and colour of foliage in *Robinia pseudacacia*, an endotrophic species. The experiments were carried out in sterilized Wareham soil in order to ensure the absence of nodule-forming organisms which had previously been recorded for

certain parts of the Wareham area and which, in earlier studies, had been suspected of masking the effect of mycorrhizal fungi. Within 6 weeks from sowing, the inoculated cultures showed a remarkable change in colour from pale green to a dark green, and, after an additional 9 weeks, growth stimulation was also noticeable (Plate V, Fig. 4). The experiments with *R. pseudacacia* are still in progress along with similar experiments in which other endotrophic tree species are being tested in their reaction to *Boletus scaber*.

So far, while ectotrophic mycelia were observed to improve growth of certain endotrophic trees, the converse relationship, stimulation of ectotrophic plants by endotrophic mycorrhiza formers, has not been demonstrated.

During the course of these investigations, experiments had been started using *Ailanthus glandulosa*, believed to be a non-mycorrhiza-former (4), as a test plant for the activity of free-living mycorrhizal mycelia. It was however observed that, as regards its mycorrhizal habit, the species is not different from other forest trees and, under certain soil conditions, is capable of forming typical endotrophic infections.

DISCUSSION

In the experimental studies concerned with the effect of free-living mycorrhizal mycelia on the development of tree seedlings, the following fungal species were tested: *Rhizopogon luteolus*, *Boletus scaber*, *B. bovinus*, and *B. elegans*. No growth stimulation of the higher plant could be observed with certainty in the case of *B. bovinus* and *B. elegans*. Positive results were recorded in the case of *Rhizopogon luteolus* and above all with *Boletus scaber*.

The nature of the influence exercised on seedling growth by the mycelia of *B. scaber* and *Rhizopogon luteolus* is not indicated by the experimental results and no attempt has been made yet to analyse the external activity of these two mycelia. The effects produced might be due to substances similar to those observed by Slankis (9) to induce dichotomous branching in pine roots. It is also suggested here that *Boletus scaber* and *Rhizopogon luteolus* may act by attacking and decomposing organic matter in the soil and in this way set free nutrients just as any white rot would do.

Boletus scaber and *Rhizopogon luteolus* can probably be grouped among the transitional ecological types of soil mycelia on the boundary between obligate mycorrhiza-formers and litter-decomposers. They may behave not unlike *Boletus subtomentosus*, which Romell (8) found to be a facultative mycorrhiza-former and which, as Lindeberg (5) demonstrated later, is capable of acting as a litter-decomposing fungus. Lindeberg also found that *B. subtomentosus* produces great amounts of polyphenol oxidasis, an enzyme often observed in connexion with the breakdown of cellulose and lignin. It is of interest to find in Lindeberg's list of data for oxidase reaction of a number of mycorrhizal fungi, that *B. scaber* and *Rhizopogon luteolus* formed traces of this enzyme, while no oxidase reactions are recorded for *Boletus bovinus* (*B. elegans* was not tested).

A further indication that *B. scaber* is rather atypical among the mycorrhiza-formers comes from results of experiments carried out by Handley (2), who

demonstrated that certain extracts from *Calluna* raw humus cause total growth inhibition of a number of mycorrhizal mycelia. Among the fungi tested, *Boletus scaber* was the only mycelium not affected by the toxic extract.

From recent observations on the reactions in pure culture, it has also become increasingly apparent that *B. scaber* behaves differently from the majority of mycorrhiza-formers. The mycelium shows hardly any specialized demands. It makes vigorous growth on the common culture media tested so far; it develops within a wide range of pH, and grows freely submerged in liquid media. (A detailed account of pure culture behaviour is in course of preparation.)

From the evidence available at present, we cannot conclude that *B. bovinus* and *B. elegans* are unable, under different conditions, to produce rhizosphere effects similar to those recorded for *B. scaber* and *Rhizopogon luteolus*. Only one type of soil, a *Calluna* heathland soil of poor quality, was used as growth medium and only a few species of trees were employed as test plants. Moreover, inoculation by active mycorrhizas or by sporophores may be more suitable than introduction from a pure culture. Mycorrhizal roots are particularly effective inocula, but difficulties as regards their use arise from the fact that roots associated with mycelia of known identity are not easily available. Mycorrhizas formed by *Mycelium radicis nigrostrigosum* are readily recognized and for this reason would be a convenient material for inoculation. It is evident from the foregoing studies that mycorrhizal fungi *per se* can play a definite role in the development of forest trees and that, in some contexts at least, their influence is beneficial. It would be a difficult task to differentiate generally between the effects originating from the rhizosphere activity of the mycelia and those arising from the infection itself. But while the distinction is important academically, it should be of little consequence in forestry practice.

LITERATURE REFERENCES

(1) Burges, A.: 'On the Significance of Mycorrhiza.' *New Phytol.* xxxv. 117–31 (1936).

(2) Handley, W. R. C.: Unpublished data cited by J. L. Harley in 'Associations between micro-organisms and higher Plants (Mycorrhiza)'. *Ann. Rev. Microbiol.* vi. 367–86 (1952).

(3) Levisohn, I.: 'Growth Response of Tree Seedlings to Mycorrhizal Mycelia in the Absence of a Mycorrhizal Association.' *Nature*, 172, 316 (1953).

(4) ——: *Report on Forest Research for the year ending March 1953*, 102–3. H.M. Stationery Office (London, 1954).

(5) Lindeberg, G.: 'On the Occurrence of Polyphenol Oxidases in Soil-inhabiting Basidiomycetes.' *Physiol. Plant.* i. 196–205 (1948).

(6) Melin, E.: 'Experimentelle Untersuchungen über die Birken- und Espenmykorrhizen und ihre Pilzsymbionten.' *Sv. Bot. Tidskr.* xvii. 479–520 (1923).

(7) Rayner, M. C., and Neilson-Jones, W.: *Problems in Tree Nutrition* (London, 1944).

(8) Romell, L. G.: 'Barrskogens marksvampar och deras roll i Skogens liv.' *Sv. Skogsvårdsföreningens Tids.* 348–75 (1939).

(9) Slankis, V. 'Einfluß von Exudaten von Boletus variegatus auf die dichotomische Verzweigung isolierter Kiefernwurzeln.' *Physiol. Plant.* i. 390–400 (1948).

(10) Wilde, S. A.: *La Symbiose des Arbres et des Organismes inférieurs: Sa Nature et son Importance en Sylviculture.* Rapports et Communications à la Section 13. 123–6. Huitième Congrès International de Botanique (Paris, 1954).

(11) ——: 'Mycorrhizal Fungi: Their Distribution and Effect on Tree Growth.' *Soil Sci.* lxxviii. 23–31 (1954).

THE PATTERN OF MIXTURES

By L. C. TROUP and D. R. JOHNSTON

SUMMARY

The authors consider the main reasons which may justify the planting of mixtures rather than pure crops, e.g. the provision of nurses, intermediate returns, continuity of employment, biological considerations, health, fuller utilization of the site, improvement of form, &c., and give four examples of possible patterns for mixtures in strips to suit varying circumstances.

WHEN mixtures of two or more tree species are grown together they may be planted in a variety of group or strip patterns and the object of this article is to consider, in the case of strip planting, how the spacing of each species within the plantation is related to the silvicultural and economic aims of the planter. To this end it will first of all be advisable to consider briefly the reasons for planting mixtures.

1. *To supply a nurse for a tender species*

The nurse species may, in general, be regarded as an artificial seral stage, introduced in order to obtain an approximation to forest conditions so that a valuable species may be enabled to establish itself under what would otherwise be adverse conditions. The nurse may act through the soil, the existing vegetation, or the atmosphere and when deciding upon a nurse, it is important to be quite clear what particular site factors require to be ameliorated. These may include low temperatures, high temperatures, evaporation, competing vegetation, reducing conditions in the soil, &c. The effect of reduced light in improving the form of beech (*Fagus sylvatica* L.) may also be included under this head (1).

The following example demonstrates an early nursing effect of Scots pine (*Pinus sylvestris* L.) upon Sitka spruce (*Picea sitchensis* Carr.) when grown in mixture on a *Calluna* heath. It may be noted that there are also long-term benefits in this case depending upon the deeper rooting habit of the pine with a consequent improvement in some physical properties of the soil (3).

Age of Sitka spruce	*Pure Sitka spruce Length of leading shoot*	*Sitka spruce and Scots pine Length of leading shoot*
7 years . .	8 inches	9 inches
14 years . .	2 feet 2 inches	7 feet 7 inches

In this particular case the Scots pine probably achieved its nursing effect in the elimination of the *Calluna*, which is a severe competitor for nitrogen. A pine strip of several rows is more effective in suppressing ground vegetation than a single row admitting light to the ground from both sides. The provenance of the nurse species may be important as, for example, in the case of Lodgepole pine (*Pinus*

contorta), the coastal variety of which has a far denser foliage than the better-formed inland type and is therefore more effective in suppressing subordinate vegetation (4).

2. *To supply an intermediate financial return*

When calculating the cost of producing timber, the early expenses of establishing and maintaining the plantation may be carried forward at compound interest until the original investment has been recovered, when it is justifiable to regard the stand as a cellulose-producing factory, run on a simple interest basis. For this reason any financial return in the early years of the plantation is especially valuable. A conifer producing a valuable product at an early age in the form of pitwood, pulpwood, or poles for fencing and rustic work, &c., is frequently planted in mixture with a hardwood for this purpose. As an example the case of Douglas fir (*Pseudotsuga taxifolia* Brit.) and *Thuja plicata* planted under cover in mixture with beech may be quoted. In this instance, the conifer is planted solely for economic reasons. It may be as well, at this stage, to consider the argument that this object may be more easily achieved by planting part of the area with a pure hardwood and part with a pure conifer crop. This argument is fallacious from a purely economic point of view because the early thinning from the pure hardwood crop would be unsaleable, while if the trees were planted at such a wide spacing that no thinnings were necessary before the trees were of an economic size, the land would be incompletely exploited throughout the early years of the plantation and the trees would tend to become very branchy.

3. *To prevent soil degradation*

On the less fertile sites, beech and most conifers, if grown pure, may tend to form a raw humus and ultimately produce a podzol profile with all its attendant disadvantages. This risk may be lessened by growing a 'mull-forming species' in mixture with the 'mor-forming tree'.

4. *To equalize labour requirements*

This follows from (2). When a new forest is created, there is a great deal of work in the early years, due to planting and weeding, but this is followed by a longer or shorter period of reduced labour requirements. This labour redundancy will be reduced if there is in mixture a proportion of trees furnishing early financial returns and, therefore, requiring labour for felling, trimming, extraction, and the preparation of produce.

5. *To insure against the biological or economic failure of one species*

There is a fundamental difference between these two conceptions. An economic failure due to changing fashions or demands may, from a purely economic point of view, be as well provided against by planting subsidiary species in pure blocks, but a biological failure due to an unfortunate choice of species, an exceptional spell of weather, or an epidemic, is a different matter. Such a failure may occur at any time in the life of the crop and, provided it occurs after canopy has formed, the surviving species may occupy the site fully, depending upon the planting

pattern which has been adopted. This conception of insurance has been invoked to justify the dilution of beech with conifers due to the possibility of severe squirrel damage in the future.

6. *To dilute a scarce species*

There would be little advantage from an economic point of view, in diluting a species which affords valuable returns from an early age, e.g. larch, because in this case, if the number of plants were limited, they would afford a not very dissimilar return whether planted in a pure block over a certain area or in mixture with another species over double the area. If, however, the scarce species affords little return in the early years, it is a waste to plant it pure, since under such conditions a large proportion of the plants serve little purpose other than to assist in the self-pruning of the final crop trees and to suppress the ground vegetation, and these functions might equally well be achieved by a more plentiful or less scarce species. In practice a diluent would be chosen able to produce an economic return when removed from the plantation. For this reason it is difficult to separate objectives (3), (4), and (6).

7. *To promote health*

This is a less tangible objective, but it is a matter of common experience that mixed forests are less liable to epidemics than pure forests. There are, no doubt, various reasons for this. It has been suggested that the predatory population is less at the mercy of sudden variations in the number of its insect victims, and birds are said to be more numerous in mixed plantations, especially mixtures of hardwoods and conifers. In addition, fungal spores have a smaller chance of coming into contact with a susceptible host and there is also some evidence that under certain conditions the individual trees are more vigorous.

8. *To exploit the site more fully*

A great deal of investigation has been carried out by Continental foresters, e.g. Vanselow (5), to determine whether the increment of a mixture is greater than that of a pure crop. The evidence suggests that the total volume production is intermediate between that of pure crops of the component species, although the dry matter increment of a mixture may be greater than that of either component pure. It seems reasonable to suppose that if there is a greater increment in a mixture, it will occur on a marginal site where the shortage of a particular nutrient might become limiting for a pure crop, whereas the demands of a mixture for any one nutrient at any given time of the year are likely to be less intense.

9. *To exploit variation in the site*

If the site is not uniform, the variations may be exploited by varying the species to suit the micro sites. For instance, on an undulating heathland in East Anglia, Corsican pine (*Pinus nigra* var. *Calabrica* Schneid.) was the main species, while Scots pine was planted in the small frosty hollows.

10. *To obtain a dense canopy*

It was an axiom of classical Continental forestry that a plantation should have

a closed canopy and a heavy leaf-fall. For this reason it was considered desirable to mix shade-intolerant pioneer species with a shade-bearing understorey. Modern practice accepts the viewpoint that such a technique facilitates natural regeneration by suppressing the ground flora and by conserving moisture at the soil surface. Moreover, the growth potential of the site is limited and any given area can support only a limited photosynthesizing surface area. Light, water, nutrients, and space utilized by the ground flora are therefore a loss to the forester. The higher humidity beneath the canopy is believed to accelerate the decay of suppressed branches, thereby producing cleaner timber. It may also be a fact that the organisms responsible for some stages of litter breakdown are favoured by a moist and relatively cool atmosphere. This is unlikely to apply, however, to the northern coniferous forests where temperature rather than moisture is likely to be a limiting factor.

11. *To improve the form of one species*

This may be regarded as an aspect of objective (10). For instance, a proportion of beech is maintained in the Continental oak forests partly to maintain a clean forest floor and partly by their shade to suppress the side branches of the oak. It is the aim of present-day beech silviculture in this country to reduce the light intensity over the beech to as little as 20 per cent. of full light in order to induce a better form in the growing trees. This effect is probably due to the inhibition of late growth which, being susceptible to weather, insects, and fungi, is easily damaged. Such damage frequently induces multiple leading shoots (1).

12. *To facilitate natural regeneration*

It has already been mentioned that mixtures of light demanders and shade bearers may facilitate natural regeneration by suppressing the ground flora and increasing the humidity at the soil surface. In addition, the seeds of some species will establish themselves only under the shade of a different species. For instance, in the spruce-silver fir forests of central Europe, the spruce establish themselves under the fir and the fir under the spruce.

13. *To prevent windthrow*

If the desired species is liable to windthrow, it may be necessary to plant in mixture with it a deep-rooting windfirm species.

14. *To improve the amenity value*

The monotony of large areas of pure plantations may be relieved by planting in mixture, a contrasting species. An evergreen with a deciduous species. A conifer with a hardwood. An early flushing with a late flushing tree. A dark sombre foliage with a light leaf colour.

FACTORS GOVERNING PATTERNS

An examination of the reasons for planting mixtures shows that the biological advantages are likely to be most pronounced in a very intimate mixture. Practical foresters will be aware, however, of the serious silvicultural and management

problems connected with such mixtures. The growth rates of different species are only by chance comparable on any given site and when two species are planted in a one row/one row mixture, there is a danger that one species may be suppressed by the other, or that expensive and uneconomic tending operations will become necessary in order to save that constituent which, though slower growing in youth, may be the species better adapted to the site and capable, ultimately, of affording the more valuable product. Furthermore it is frequently desirable to maintain the nursing effects of the subsidiary species for as long as possible. If it becomes necessary to destroy the nurse in order to save the principal species from suppression, the potential value of the long-term nursing effect is destroyed.

If it were possible to assess accurately the potentialities of different species on different sites, it would on occasions be possible to plant one row/one row mixtures with more confidence as to the outcome. As it is, however, the relative growth rates of two species of tree may be changed by quite small variations in the soil, rainfall, exposure, or aspect. For instance, on the somewhat drier soils of the South Downs beech will suppress larch, while on patches of heavier clay with flints the larch soon overtops the beech.

For these over-riding reasons it is usually considered desirable that each species, and particularly the species destined to form the final crop when the second constituent is acting as a nurse, should be planted in strips not less than three rows wide so that a proportion at least of the trees shall grow surrounded by their own kind.

This consideration is strengthened by what may be called 'anticipated neglect'. It must always be at the back of the forester's mind that the more his plantation depends upon future tending operations, the less likely are they to succeed. It is to be hoped that such will not be the case in the future, but there is nevertheless ample evidence in this country of good intentions marred by subsequent neglect due, frequently, to economic or political changes. From such considerations has arisen the fashionable three row/three row mixture of hardwood and conifer, the latter species usually intended primarily as a nurse and an economic diluant or, when planted under cover, simply to provide an early financial return without reducing the ultimate stocking of the final crop. Less often the roles are reversed and the conifer is diluted with a hardwood to preserve the fertility of the site.

Although the available evidence suggests that it is risky and expensive to raise a one row/one row hardwood conifer crop, it is probably not impossible to protect the hardwood from the risk of damage and suppression by pruning, and finally felling, of conifer nurses. If, however, instead of a one hardwood row/one conifer row or a three hardwood row/three conifer row, one were to plant a one hardwood row/three conifer row mixture, the volume of the conifer timber produced would be increased by 50 per cent. and this might possibly justify a considerable outlay in maintaining the balance between the final crop hardwood and the intermediate crop conifer.

So far as the practical application of these theoretical considerations is concerned, there are basically two types of mixture: those in which the constituent species have roughly equal rotations and those in which the life span differs. In

the first case, the final crop is likely to be weighted in favour of the species most suited to the site, but a high proportion of the subsidiary species may remain. In the second case, the final crop may consist entirely of the species which is thought to have the longest rotation. Between these two extremes all degrees of variation are possible. In planning a mixture, it is necessary to consider most carefully the rotations of the species concerned on the particular site to be planted. Armed with this information, it becomes possible to work out in detail their espacement at the time of planting and the likely development of the entire crop throughout its rotation. Normally one of the species in a mixture is regarded as the major final crop tree and any planting pattern which fails to give adequate selection and full final crop stocking of the major species can be considered to have failed. The subsidiary species, for whatever reason it is planted, must be so espaced as to fulfil its function completely within the limits of the line mixtures under consideration.

The foregoing paragraphs can be summarized in three questions which the forester should ask himself:

What are the likely rotations of the constituent species?

Which is to be the major tree and what is the planting spacing which will give adequate selection?

What is the espacement of the subsidiary species which will best fulfil the objective?

In framing replies to these questions, it is necessary to keep in mind the likely number of final crop trees. Local knowledge may be helpful and a general rule evolved by Hummel, that the radius of the crown in feet is equal to the quarter girth expressed in inches, may be useful in some instances. However, it is always best to examine a well-grown crop on a comparable site and to deduce the final crop spacing therefrom.

Several examples may help to make the foregoing consideration clearer.

Example 1

On London Clay it is intended to raise a crop of pedunculate oak (*Quercus robur* L.) with a Norway spruce (*Picea abies* Karst) nurse to give some protection from frost and to provide an early return. It is considered that 140 years is the likely oak rotation and that the bulk of the Norway spruce will have been removed by the 80th year. At this stage the spacing of the oak should be appropriate to a pure crop aged 80 years. It is considered that about 150 oaks per acre should remain, i.e. an average spacing of 17 feet; the Norway spruce should therefore be confined to strips about 17 feet wide. In order to give full scope for selection in the oak, three rows might be planted. The Norway spruce if spaced at $4\frac{1}{2} \times 4\frac{1}{2}$ feet would also consist of three rows, the outer oak rows then being 18 feet apart near enough to the theoretically desirable espacement of 17 feet to be acceptable.

The outer Norway spruce rows would be removed gradually as they threatened good oak; a proportion might go for Christmas trees at a quite early stage. Later, useful coniferous thinnings would be available. In the 40th or 50th year most of the trees in the outer Norway spruce rows would have been removed, but many

trees in the centre rows would remain. At this stage too, the hardwood thinnings would be getting to a very useful size. In the 80th year most of the Norway spruce would have gone, but a few fine specimens might remain to go on with the oak. This is a satisfactory life history and the planting spacings are, therefore:

Oak: Three rows at 4×4 feet
Norway spruce: Three rows at $4\frac{1}{2} \times 4\frac{1}{2}$ feet
} with $4\frac{1}{2}$ feet between adjacent Norway spruce and oak rows.

Example 2

On a sandy loam it is decided to plant sessile oak (*Quercus petraea* Liebl.) in mixture with European larch (*Larix decidua* Mill.). The oak and European larch rotation are respectively 160 and 80 years. In the 80th year it is considered that the sessile oak should number about 220 to the acre; this implies an average spacing of 14 feet. It follows that the European larch strips should not occupy more than 14 feet of ground. As a light demander and a tree that does best under a heavy thinning régime it must be given space along the rows since it cannot be given scope across them. In this case three rows of larch might be planted at a spacing of 4×8 feet, the centre row being staggered with respect to the two outer rows. This mixture, which has actually been used, should produce very useful early thinnings from the outer rows with a proportion of the centre row going on to timber. After the 80th year only a few good larch will remain, but well before that the oak thinnings will provide saleable material.

Example 3

On a thin rendzina soil, it is decided that beech is to be the final crop tree with Corsican pine as a nurse. The beech rotation is placed at 120 years and it is known that Corsican pine will not survive to more than 50 years under these conditions. Since there is no point in waiting until the Corsican pine die, it is decided to make their rotation 40 years. At this stage the beech, it is thought, should not be more than 8 feet apart. Clearly the Corsican pine strips should only be 8 feet wide and this implies only one row of Corsican pine, but herein lies a danger. If only one row of Corsican pine is planted, it might be necessary to remove all the trees *well before the 40th year* in order to prevent them swamping the beech. The same objection applies to two rows of Corsican pine. Apparently the system breaks down, for if three rows are planted and all are removed by the 40th year then the beech will be farther apart than the desired 8 feet, and furthermore, blank alleys might divide the beech strip. In this case there are two alternatives, either one rejects the line system or one knowingly accepts its limitations. Here one might plant three rows of Corsican pine at a narrower lateral spacing than is normal, spreading them out along the lines by way of compensation. A compromise solution would be as under:

Three rows of beech at $4\frac{1}{2} \times 3$ feet, with $4\frac{1}{2}$ feet between adjacent beech and Corsican pine rows.

Three rows of Corsican pine at $2\frac{1}{2} \times 8$ feet, the two outer rows being staggered with respect to the centre row and leaving the Corsican pine $4\frac{1}{2}$ feet apart.

The outer beech rows would thus be 14 feet apart against the theoretical ideal

of 8 feet. If, however, a proportion of the Corsican pine are now allowed to go on beyond the 40th year, the situation may be much improved. It may even be found desirable to allow some Corsican pine to remain until they are on the point of dying. On difficult soils one must always envisage such problems as this and the answer will often be a compromise.

The three examples given have considered only two species in the mixture. Since these are more usual, the aims of management can usually be so achieved. It is, however, quite possible and often desirable to use three or four species. Sir Richard Cotterell (2) has produced an interesting example consisting of oak, larch, sweet chestnut, and ash planted to a carefully worked out pattern. Less complicated mixtures may often suggest themselves for either silvicultural or economic reasons. Thus on the downland soils of Sussex, Scots pine usually does better than Corsican pine initially but does not live so long. One might well have the early growth and hence quick nursing effect of the Scots pine and at the same time the longer rotation of Corsican pine by planting two outer rows of Scots pine and a central row of Corsican pine. This could be applied to Example 3 above. On the economic side it is often possible to 'sandwich' in Norway spruce for the sole purpose of providing Christmas trees. It is beyond the scope of this paper to do other than indicate the possibilities. The precise constituents of each mixture will depend upon local conditions.

Example 4

It has been explained earlier that there is evidence to show that alternate row mixtures can be successful in some instances, their main disadvantage being that one species has to be removed almost entirely at a relatively uneconomical age. This results in light early returns only. It is possible however to envisage a mixture consisting mainly of the nurse or early-return species with only single rows of the final crop species. An example would be a beech/Scots pine one/three row mixture. Compared with a three/three row mixture, this would increase the conifer yield by 50 per cent. while compared with a one/one row mixture the increase would be more than 50 per cent. due to the longer expectation of life of the centre rows of conifers.

The two outer rows of Scots pine would have to be treated in exactly the same way as in an alternate row mixture and would be removed almost entirely at an early stage. The centre row would go on for much longer and one might envisage a rotation of 60 or 70 years with a few good Scots pine remaining longer. Since the bulk of the conifers would be removed by the 60th or 70th year, one might consider that at that age the beech should not be more than 15 feet apart. Therefore one would allow 15 feet for the three conifer rows. The suggested spacing might be:

One row beech with the trees 3 feet apart (a close spacing to allow for greater ultimate selection).

Three rows Scots pine at 5×5 feet with 5 feet between adjacent Scots pine and beech rows.

Other conifers or mixtures of conifers could be used equally well, or to greater

advantage on some sites. The middle row of conifers might well consist of a different species from the outer rows. Thuya, tsuga, or Lawson cypress may often be a sound choice for the longer rotation of the central row. This example is offered tentatively for consideration rather than for uncritical acceptance. Its advantages and disadvantages are summarized below:

Advantages

(*a*) The early returns are greater than in any other mixture considered in this paper.
(*b*) Unproductive hardwood thinnings are much reduced.
(*c*) Compared with a one/one row mixture the maintenance is less onerous.
(*d*) The nursing effect is probably better than that obtained in a three/three row mixture.

Disadvantages

(*a*) Compared with a three/three row mixture maintenance is heavier and delays or mistakes more likely to nullify the ultimate aim of raising a hardwood crop. Very careful selection of the nurse must be made and even then one cannot guarantee that its rate of growth will not too greatly outstrip that of the hardwood.
(*b*) There may not be enough selection in the hardwoods to ensure a first-class final crop. As first-class stocks become more generally available this disadvantage may be greatly minimized.
(*c*) The coniferous leaf-fall may degrade marginal sites more than the other mixtures considered; but if this be the case, beech leaf litter would prove equally damaging. Where the maintenance of soil fertility is in question the problem is best considered as one for the correct choice of species. The pattern of the mixture can then be reviewed in that light.

LITERATURE REFERENCES

(1) Brown, J. M. B. (1953): *Studies on British Beechwoods*. Forestry Commission Bulletin No. 20.
(2) Cotterell, Sir R. (1951): 'Planting of Hardwoods in Mixture.' *Quarterly Journal of Forestry*, xlv. 154–5.
(3) Forestry Commission. Report on Research for 1941–2 (unpublished).
(4) Macdonald, J. A. B. (1954): 'The Place of *Pinus contorta* in British Silviculture.' *Forestry*, xxvii. 25–30.
(5) Vaneslow: 'Die Kulturversuche der Badischen forstlichen Versuchamstatt auf dem Köcherhof.' *Allg forst und Jagd*, 113: 33–57, 88–97, 114–28, and 148–61.

REVIEWS

Der heutige Stand unseres Wissens vom Humus und neue Wege zur Lösung des Rohhumusproblems im Walde. By W. Wittich. *Schriftenreihe der forstlichen Fakultät der Universität Göttingen*, Band 4. J. D. Sauerländer's Verlag, Frankfurt am Main, 1952. Pp. 106.

Mull and Mor Formation in Relation to Forest Soils. By W. R. C. Handley. Forestry Commission Bulletin No. 23. Her Majesty's Stationery Office, London, 1954. Pp. 115. Price 10*s*.

Review by L. G. Romell

STUDYING Danish beechwood soils in the seventies and describing mull and mor as two contrasting types of an uppermost soil horizon, the seat of humus formation, P. E. Müller was well aware of the amount and importance of organic matter in mull and he emphasized the need of leaf-litter covering the soil, supporting the humus formation and keeping the mull from degrading and eventually changing into mor. Later, German workers led by Ramann forgot about the high totals of organic matter contained in mulls and took mor to be an accumulation of 'raw humus' bound to occur when the annual litter-fall exceeds a critical value. This view was quickly adopted by forest soils men and developed by some to the extreme point of stating: 'by far the best forest humus is the kind that is never produced' (H. Süchting, 1922). Meanwhile the chemical study of humus made little headway. In the thirties a leading authority took stock of the available evidence and, even though granting the importance of soil humus, discredited the very notion of 'humus' in the old sense of the word.

Ramann interpreted mull and mor as expressing different overall rates of decomposition. This simple idea, excellent for teaching, survives in textbooks and papers to the present day although more than 20 years ago it was shown to be wrong. Lack of chemical knowledge has contributed to preserving it. Only recently has progress in humus chemistry again given more individuality to the true humus, thus preparing a return to older ideas as to the nature and formation of humus. The effect of this in the field of forest soils is strikingly illustrated by Professor Wittich's important memoir, most fittingly supplemented by Dr. Handley's equally important monograph. In both, the return to P. E. Müller is noteworthy and gratifying to Scandinavian workers.

Wittich remarks that recent work in humus chemistry has given a clearer and as a whole a simpler picture of the humus proper. He rightly refers to the work of J. Hudig in Holland as fundamental. Reference could well have been made also to the experimental work of P. Thénard in the years around 1860 and to its correct interpretation by Dumas, and further to Sante Mattson's paper on proteinated complexes (*Soil Science*, 1931) whence came the idea of a humus complex comparable to tanned leather. Two main results stand out from this and more recent work: nitrogen has a central role in humus formation, and quinoid structures are essential in building up the humus complexes. The formation of such complexes is favoured by a high base status and by the action of worms.

Opposing the teachings of Ramann and Süchting as well as of Erdmann, Wittich holds that large stores of humus should be maintained in order to keep forest soils productive.

Having studied the liming experiments made in Ebnath, Adorf, Syke, Sauerlach, and elsewhere, he concludes that the important effect of lime has been to help producing and maintaining a large enough store of stable humus in the soil. It may be necessary to supply nitrogen along with the lime. This is shown by Hassenkamp's experiences in Syke.

Wittich is not concerned with mull and mor. He distinguishes 'mild' humus from 'moderately acid' and 'strongly acid' and writes: 'The formation of unfavourable humus covers is always a consequence of too low a base content of the soil.' This does not agree with evidence collected in Denmark and elsewhere. A higher nitrogen content is reported by Wittich as a further characteristic of 'mild' humus.

The problem of mor formation, barely touched by Wittich, is discussed by Handley on the basis of an extensive review of literature, surveying the differences that have been taken to exist between mull-forming and mor-forming sites, climates, or plants, and scrutinizing available data on differences between mull and mor as to the course or rate of biological and chemical processes. The general result of this penetrating analysis is remarkably negative. Few if any of all the differences reported were found constant. Vegetation appears as the most important single complex of factors favouring the formation of mull in preference to mor, or the reverse. Yet a careful review of available facts seemed to show that none of the known characteristics of litter could serve to distinguish mor-forming plants from other plants.

Looking farther for attributes of litter that could possibly be held likely to determine the formation either of mull or of mor, as the case may be, Handley discovered remarkable differences between kinds of leaf litter as to the order in which their tissues are consumed by decomposing micro-organisms. For instance, while in decomposing leaves of *Ilex* the mesophyll quickly disappeared leaving the vascular tissue apparently unaltered, the reverse was found in decomposing leaves of *Calluna*. An explanation of these unexpected facts was sought in extensive series of tests and experiments. From the results it appears that the mesophyll tissues resisting decomposition, as in leaves of heather, may do so by virtue of a tanning effect like the one suggested by Sante Mattson in 1931 for proteinated complexes resisting decomposition in the soil.

The findings might furnish a clue to the formation and some of the characteristics of heather mor, 'astringent humus' as it was called by Th. Hartig in 1840. For a possible wider application of the findings it is natural to think in the first place of hemlock mor and similar, very acid, greasy types of mor, where phenolic compounds contained in the litter may not be broken down, the pH being too low for soil white-rots to grow. One or more compounds thus persisting may exclude parts of the mull fauna and set going a circular process of mor formation, and possibly start at once a rapid podsolization, as seen under hemlock and, in experiments by C. Bloomfield, in soil columns under various kinds of litter.

It is difficult to believe that the same mechanism is at work generally in mor formation. No attribute of plant debris can reasonably be taken to account for facts such as the increasing tendency to mor formation observed with increasing age of forest stands, as under old beech in Denmark. This points instead to a competitional factor in mor formation. Indeed there are good reasons for believing that no single clue to mor formation can be found. A complicated biological equilibrium such as that of a mull can be overthrown by a number of interferences and mull must be excluded under a variety of conditions not permitting the organisms active in mull to thrive and to do their work.

The Volume-Basal Area Line. By F. C. Hummel. Forestry Commission Bulletin No. 24. H.M. Stationery Office, 1955. Price 9*s*.

Review by H. M. Steven

In recent years the Forestry Commission has issued a number of publications by Dr. Hummel and his colleagues that are of wide interest and utility, such as 'General Volume Tables' for a number of species, and 'Revised Yield Tables for Conifers in Great Britain'. Those with a special interest in mensuration have been looking forward to the next step, the publication of the methods used to compile them. Part I of the present publication presents such information for the volume tables. Part II deals with a different aspect of the same problem, and leads to the first public issue of general tariff tables which are likely to be a great use to the practising forester in the estimating of volumes of his crops. Thus while this publication is caviare for the specialist in forest mensuration, it provides the basis for aids of general use to all foresters. The tariff tables, published in an Appendix, will no doubt be issued separately in a more convenient form.

Part I is entitled 'The volume-basal area line for heterogeneous tree populations', and deals with methods of preparing general volume tables. The Forestry Commission decided to prepare such for the principal conifers in use, based on breast-height girth and total height, omitting the third variable taper for the sake of simplicity. Material was available from diverse sources, permanent and temporary sample plots, &c. Chapter 1 describes various trials made, using different formulae. In the end a formula devised by the author, $Y/H = a+bX$, where Y = volume of tree, H = total height, X = basal area, and a and b are constants, was selected. This was used to construct a volume table for Scots pine, which was tested, proved satisfactory, and was published in 1950. When this method was applied to European larch, however, it did not prove satisfactory and this led to the investigation of the use of the volume-basal area line for heterogeneous populations of trees.

Chapter 2 deals with the theoretical considerations arising from the use of the volume-basal area line for volume table preparation. The first point to be determined was whether, for a given total height, the regression of volume on basal area was linear, which relationship has been used by other workers in this field. This was tested for the seven conifers in common use in Britain, and the data presented show that this is approximately so. It follows, therefore, that $Y = a+bX$, Y being the volume, X the basal area, 'a' the regression constant and 'b' the regression coefficient. The data indicated also that 'a' and 'b' vary with height, thus giving a polynomial equation

$$Y = a_1+a_2H+a_3H^2+a_4H^3+\ldots+b_1X+b_2XH+b_3XH^2+b_4XH^3+\ldots.$$

This can be simplified if the regression of 'a' or 'b' or both on height is linear, and with a further simplification if the constants a_1 or b_1 are zero. If all the simplifications are possible one gets the formula used for the calculation of the Scots pine volume table given above. The volume table could thus be calculated by starting with the simplified formula and adding terms until a further addition results in no significant increase in precision. This would have been the most mathematically correct procedure, but the author for a number of reasons preferred to carry out the preparation of the volume table in the following steps:

1. Within each height class determine (graphically or by calculation) the linear regression of Y on X.
2. Using the values of 'b' so obtained determine the regression of 'b' on H.
3. Similarly determine the regression of 'a' on H.
4. The adjusted values of 'b' and 'a' so obtained are used for the construction of the volume table.

Chapter 3 describes the application of this procedure to European larch, Norway spruce, Corsican pine, Sitka spruce, Douglas fir, and Japanese larch. In applying the method, it was found that the regression of '*b*' on *H* was linear for most species. Only Sitka spruce gave difficulty and it was decided that until more data were available for this species, the Norway spruce table could be used for it. The regression of '*a*' on *H* was more variable. In general it is concave in form in the lower height classes and there may be a point of inflexion near the upper limit of the height range. A study of the material suggested that the form of the general volume equation is likely to be:

$$\hat{Y} = a_1 + a_2H + a_3H^2 + b_1X + b_2XH,$$

but there may be additional terms, a_4H^3 and a_5H^4.

Part I is a definite contribution to the methodology of volume table preparation. There still remain problems to be investigated. For example, in Sitka spruce the value of '*b*' in the largest two height classes is less than in the smaller. Thus in the largest girths an increase in height is correlated with a reduction in volume. This would be so if the largest trees exhibited greater taper. The author suggests certain reasons why this may be so, but it is more likely due to the largest trees being subject to much greater wind pressures on their crowns which would tend to have this effect. If this is so, it would also be interesting to check on the applicability of the volume tables to extreme sites, particularly as regards wind exposure.

Part II deals with the volume-basal area line *within* a stand, more particularly pure, even-aged coniferous stands. The work of other investigators has shown that the regression of tree volume on basal area within a given stand is approximately linear, and moreover is so *irrespective* of height, and therefore unlike that in heterogeneous tree populations. The contribution of the author is his investigation into the influence of species, site, age, and thinning treatment on this relationship. In order to compare these effects, it was necessary to obtain an estimate of the precision attained and this is dealt with in detail in Chapter 4. The material used was the data from the Forestry Commission permanent sample plots for the same seven coniferous species, particularly the comparative thinning plots that had been measured a number of times, and beginning with the well known replicated Bowmont plots for Norway spruce.

The results are presented in Chapter 5. As the regression of volume on basal area is usually linear, the appropriate formula is $\hat{Y} = a + bX$, the meaning of the symbols being as before. The conclusions reached are as follows: '*b*' is not affected by thinning treatment which suggests that it is not closely correlated with girth, which is; the regression of '*b*' on height is reasonably linear to a top height of 80 feet, thereafter the position is uncertain; height was chosen instead of age because the regression of '*b*' on top height was more likely to be linear than on age, and to give a better correlation with crops on different sites; the effect of varying sites and species on '*b*' is less clear, but the author concludes that the slight differences in '*b*' (for a given height) in this respect are within the limits attributable to error.

After the first investigations, the analyses were not made for '*a*' but for *z*′, where $z' = -a/b$. It was found that *z*′, unlike '*a*' remained very nearly constant irrespective of height up to a top height of about 70 feet, thinning treatment, height, and species, although some plots of Douglas fir and Sitka spruce show some divergence. This constant value of *z*′ was 0·03 square feet. The reason why it should be of this value is obscure. In young stands, as volumes of trees below $2\frac{1}{8}$ q.g. at b.h. are ignored, this would provide the explanation, but it is not clear why it should apply when the smallest trees are well above this critical girth.

Chapter 6 discusses the applications of Part II to mensurational practice. Two are put

forward. The first relates to the use of the volume-basal area line in permanent sample plot work. It will be possible to increase the precision of the volume estimates made at previous remeasurements by first determining the regression of '*a*' and '*b*' on top height, and recalculating the plot volume at each remeasurement using these adjusted values of '*a*' and '*b*' in the regression: $Y = a+bX$. Secondly, if all lines pass through the point $z' = 0{\cdot}03$ square feet only the mean point need be determined. The reviewer is doubtful whether the latter assumption should be made in sample plot investigations without further work on z, in view of the discrepancies, e.g. particularly in Douglas fir.

The second is of much wider application. It is to use the results obtained in Part II to construct so-called general tariff tables which can be used for volume determination of coniferous species, irrespective of site, provided the top height of the stand is less than 80 feet. These tables are based on regression lines all with a common intercept on the X axis ($z' = 0{\cdot}03$ square feet), and the values of '*b*' so chosen that the volume interval between successive lines is 1 hoppus foot at a basal area of 1 square foot. Thus tariff 18 shows a volume of 18 hoppus feet at a b.h.q.g. of 12 inches and so on. The method thus depends on the validity of $z' = 0{\cdot}03$ square feet.

The tariff tables so tabulated are given in Appendix III with instructions as to their use. This is comparatively simple; the only drawback is that one has to determine the volume of a number of trees in the wood in order to select the appropriate tariff number. This is best done on felled trees, but the volumes of standing sample trees can be estimated by using the general volume tables for the appropriate species. The author states also that it may be possible to select the tariff number directly from the top height of the stand, and if this proves to be so when tested it will simplify the application of the method. The use of these tariff tables has a number of advantages compared with other methods, the principal being that the estimate is obtained not only for the total volume but also for its distribution by breast height girth classes, in any degree of sub-division desired. While the general idea is not new, the author's development of tariff tables using the volume-basal area line is an important piece of work. The tables have been tested out in practice in the Forestry Commission, and in teaching work in the Universities. Their widespread use is to be commended.

The author is to be congratulated on this contribution to mensurational knowledge. It was not an easy task to present the results of this investigation. While one cannot expect a mathematical dissertation to be readable, it is both clear and concise.

Zeitschrift für Forstgenetik und Forstpflanzenzüchtung (*The Journal of Forest Genetics and Forest Tree Breeding*). Editorial Office: (24a) Schmalenbeck, über Ahrensburg, Holstein, Germany. Published by J. D. Sauerlander's Verlag, Frankfurt-am-Main, Germany. Subscription for each volume consisting of six parts—D.M. 30 (for students D.M. 24) plus postage. Vol. i, 1951; Vol. ii, 1952/53; Vol. iii, 1954; Vol. iv, 1955.

Review by J. D. Matthews

THE first issue of this periodical devoted to forest genetics and forest tree breeding appeared in August 1951. The founding editor, Dr. W. Langner (Director of the Institute for Forest Genetics and Forest Tree Breeding at Schmalenbeck), introduced the journal in his first editorial and explained how it originated. Dr. Langner felt that forest

genetics and forest tree breeding were developing so rapidly that the subject could no longer be dealt with satisfactorily in journals covering the whole broad field of silviculture. He considered that the science of genetics must stand on its own feet as a basic study in forestry as it has done in agriculture and horticulture. Dr. Langner concluded by inviting the use of the journal for the interchange of information among forest geneticists and forest tree breeders everywhere.

As befits the origin of the journal the greater proportion of the articles and abstracts published have been German, but since 1952 (Vol. ii, No. 1) there has been an International panel of editors which now consists of tree breeders from France (P. Bouvarel, Nancy), Japan (Prof. K. Sato, Fukuoka), Germany (Dr. W. Langner, Schmalenbeck), Sweden (Dr. H. Johnsson, Ekebo), and the U.S.A. (Dr. F. I. Righter, Placerville). One-quarter of the original articles of vol. iii, 1954, were by authors working outside Germany. The majority of the articles now have summaries in German, English, and French.

A glance through the pages of past issues will provide a good impression of the problems which are claiming the attention of workers in the field of forest tree improvement. The process of selection and breeding is now being used in most countries with afforestation programmes to develop new and improved varieties and hybrids of a number of tree species. German work is described by Langner (iii. 55–60); the improvement of Slash and Longleaf pine in Florida, U.S.A., is outlined by Mergen (ii. 126–9) and a brief notice of the work on *Araucaria* spp. in Argentina has been contributed by Tersdorff (ii. 90). The improvement of beech by selection and breeding is receiving considerable attention in Germany (Krahl-Urban, i. 114–20) and in Denmark (Nielsen and Schaffalitsky, iii. 6–17). The breeding of Scots pine and the larches is part of the forest tree breeding programme in many countries and articles on the work in progress in Germany and Great Britain have been contributed by Lucke (i. 74–77) and Matthews (ii. 59–65) respectively. The article on the application of forest genetics in silviculture by Von Schrötter (iii. 69–83) will interest many practising foresters and there is also in vol. iv, pp. 21–25, a good general summary of the aims and methods of forest tree improvement by Khan.

A knowledge of the mode of inheritance of desired characters and the breeding characteristics of species, types, and individuals is an essential basis of all successful breeding work. Genetical and cytological studies are now in progress in many countries. The articles of Sietz (i. 22–32 and 70–73; ii. 77–90; iii. 1–6) describing work on poplar and aspen, of Illies on abnormalities in Norway spruce seedlings (ii. 28–32), and of Zenke on meoisis in Douglas fir (ii. 96–102) show how this very important work is developing in Germany. Papers on species relationships in the pines and on some chemical aspects of the Diploxylon group of pines have been contributed by the American forest geneticists Duffield (i. 93–100) and Mirov (ii. 93–96).

The geneticists and cytologists provide the basis for successful tree breeding. The tree breeder applies this knowledge when selecting suitable parents on which to base new varieties and hybrids. The selection of apparently desirable phenotypes (or 'plus' trees) is also based upon a study of the natural variation existing in the subject species. The papers by Mudrich (ii. 32–41), Von Schrötter (iii. 33–38), and Kleinschmidt (iv. 1–15), on the crown types found in the larches are typical of the work required. Rubner (iii. 49–51) also deals with natural variation in the widest sense by describing briefly the principal ecotypes of European larch in Switzerland.

Four main breeding methods are employed in the improvement of forest trees—generally known as Selective breeding, Cross breeding, Polyploid breeding, and Inbreeding. These methods may be used to breed for yield, for resistance to disease and insect attack, for tolerance to very adverse site conditions, and for timber quality.

Selective breeding, sometimes called 'Strain building', is used for the slow seed producers such as Scots pine, Douglas fir, and beech and consists essentially of selecting plus trees, propagating them by grafting, and planting the grafts in seed orchards where seed of new varieties is produced following intensive pollination between the various clones. An essential step in this process is the testing of the genotype and breeding characteristics of the selected parent trees. This is done by a combination of clonal trials of grafted plants and trials of the progeny produced by the parent trees after free and controlled pollination. The subject of the design, layout, and assessment of progeny trials is extremely important, and a number of tree breeders have studied ways and means. The theoretical approach to progeny trials is the subject of a paper by Stern (iii. 91–98). Dr. H. Johnsson has contributed a paper on the design of progeny trials (ii. 2–8) while Schmidt and Stern (iv. 38–58) have discussed the interpretation of the results obtained from such trials. Kleinschmidt (iv. 1–15) has made an interesting analysis of the results of a trial of the progeny of selected European larch trees produced after open pollination in the forest.

Cross breeding or 'Heterosis' breeding is the method used directly in the breeding of the more prolific seed producers such as birch, alder, ash, and larch and in the later stages of work on species such as the pines and beech. Crosses are made between species (interspecific crosses) and within species (intra specific crosses). The well-known interspecies cross European larch × Japanese larch = *Larix* × *eurolepis* Henry is receiving the attention of Langner (i. 2–18 and 40–56) and Gothe (i. 108–10; ii. 122–5). De Jamblinne (iii. 126–30) reports on the early results of a cross between Scots pine and *Pinus nigra* in Belgium.

Work on breeding for resistance to disease and insect attack has been described in three noteworthy articles, namely those of Heitmüller (iii. 99–100) who is working on resistance to *Chermes cooleyi* in Douglas fir, Meyer (iii. 101–4) who reports some early results from his efforts to obtain blister rust resistance in *Pinus strobus*, and Holst (iv. 33–37) who describes his work in Canada on resistance to white pine weevil attack in Norway spruce.

Polyploid breeding—the development and use of new variants with more than the diploid number of chromosomes—is being followed up in some countries. Johnsson (ii. 73–77) has compared the growth of 9 years old diploid and triploid aspen on forest sites in Sweden. Illies (i. 36–39) describes the use of colchicine to induce polyploidy in European larch and Norway spruce and Brünig (ii. 113–17) has studied the effects of applications of B.H.C. to the roots of Scots pine. An interesting paper is that of Hyun (iii. 25–33) who describes his work in Korea on induced polyploidy in the pines.

The techniques of tree breeding have developed greatly during the 30 years since intensive controlled hybridization work began. Duffield (iii. 39–45) deals with an essential item of the tree breeder's repertoire—the handling of pollen—and Rohmeder has described (iii. 54–55) a neat 'pollen gun'. Most tree improvement workers can now use grafting techniques successfully, but the rooting of cuttings still remains a problem especially for mature trees of the larches, pines, beech, and oaks. Heitmüller (i. 100–7) describes one approach—that of the use of growth substances to stimulate root development. Lombarts (iii. 104–5) briefly describes the new 'mist' method of propagation which is proving so useful for the difficult *citrus* species in the U.S.A.

The journal is now in its fourth year of publication and the editors have fulfilled their promise to present the work of men of the two branches—pure and applied—of the young and vigorous science and art of forest tree improvement. The production of the journal is excellent—paper, printing, and diagrams all being well produced. The *Zeitschrift* is becoming a valuable source of information for tree breeders everywhere and there is also much to interest the practising forester who wishes to keep abreast of research on genetics and tree breeding.

British Mosses and Liverworts. By E. V. Watson. Cambridge University Press. Pp. xvi+419, 18 plates and 208 text-figures. 45*s*.

Review by E. W. Jones

DR. WATSON's book is the first elementary book for well over 60 years designed to enable beginners in Britain to identify mosses or liverworts; indeed it is the first such book to include both groups within the same cover.

A selection of 154 species of moss and 55 species of liverwort are treated at length, and illustrated with line drawings by the author. These illustrations, which include pictures showing habit, are good, and if used carefully they alone should enable a beginner equipped with a microscope to recognize many species. The text does not give full descriptions of these species, but emphasizes the colour, habit, habitat, and characters of diagnostic value. An additional 156 mosses and 81 liverworts are mentioned in notes which usually state briefly their differences from more common allied species. Altogether about half the British species of bryophyte are mentioned, and there is a key to these species for use with the microscope. In a pocket at the back of the book is a second key to the commoner species, for use in the field, based entirely on macroscopic characters.

Dr. Watson has made his selection of species with skill. In addition to the species which are both common and conspicuous, he has included many which are decidedly local but which are nevertheless conspicuous and abundant in their special habitats (e.g. peat moors of the Atlantic coast, mountain rocks, and springs) and hence liable to be gathered by beginners. He has obviously attempted to mention representatives of all the larger genera, and has also had an eye for the needs of the botanical student in mentioning uncommon species with some feature of special interest. A few of the species which he mentions, both common and uncommon, are inconspicuous and very unlikely to be recognized by the beginner. The forester will find that all the common woodland bryophytes are mentioned, though some (e.g. *Eurhynchium murale*, *Fissidens incurvus*) come into the category which receive scanty mention. He will not find the book adequate to identify many of the species which he may find on decaying logs, rocks, or tree boles in the Scotch Highlands or in the wetter parts of Wales or Ireland.

The ecological notes form an important feature of the book, and, though sound in general, there are a few of the statements on habitat and distribution which I personally should like to modify. Thus *Mnium punctatum* grows on rotting logs not merely in swamp woodland as Dr. Watson states, but in well-drained places, e.g. in Bagley Wood and in the Chiltern and Cotswold beech woods; and *M. marginatum*, a rare species, grows in silt on shaded river banks (e.g. by the Wye below Symonds Yat) rather than on 'mountain ledges'. *Leucodon sciuroides* is said to be 'uncommon' and *Pterogonium gracile* 'frequent' on tree boles; but *Leucodon* is not infrequent over most of England, whereas *Pterogonium* is frequent only in the west and north, and is absent from large areas. But these are exceptional examples, and every experienced bryologist is aware of the difficulty of making concise statements of general validity about habitats of common species, and of the extent to which personal experience may distort his views about the requirements of the rarer species. Taken on the whole the beginner will undoubtedly find the ecological notes, and especially the lists of species to be expected in various habitats, very helpful, but he should be aware of the limitations which may attend such statements. I well remember hesitating to accept some of my own early identifications of mosses which I had gathered around Cambridge because Dixon in his *Handbook* described their habitats as 'montane'.

The experience of beginners will provide the ultimate evaluation of Dr. Watson's book.

Many who are deterred from examining bryophytes either by their lack of access to the standard floras, or by the insistence of these latter on characters which, though reliable, can be seen only by careful microscopic observation or dissection, should find that this book provides an easier path, though those who take it must not expect to attain the certainty in correct naming, especially of those species which are not illustrated, as they could with the standard works to which it will often be necessary to turn for confirmation of tentative identifications. And they should remember that even with the help of the best books, experience and a trained eye are essential for recognizing some species.

The book should also meet the needs of those who without requiring a profound knowledge, wish to deepen their understanding of the countryside by a knowledge of its more abundant and conspicuous bryophytes. There must be many foresters in this class, for whom Dr. Watson's book can be recommended not merely as the best of its kind, but as a good and scholarly work by any standard.

Vegetation and Watershed Management. By E. A. Colman. The Ronald Press Company, 15 East 26th Street, New York, 1953. $7. Pp. 412, illustrated.

Review by R. Maclagan Gorrie

SOME excellent books dealing with forest influences have been published, notably that by Joseph Kittredge, and many more deal with the engineering phases of flood control, but this is the first major textbook to deal entirely with the water-yield value of river catchments as affected by vegetation and the treatments to which that vegetation is subjected. All the examples and data quoted belong to the U.S.A., but even within its boundaries the author gives few empirical findings. Starting his regional analysis with rainfall and pursuing it through climatic, geologic, and topographic types to the stages of water disposal he arrives at the conclusion that each catchment must be assessed on its own merits. His conclusions are in fact well worth summarizing, as they indicate the whole tone of his inquiry: 'Certain land uses and vegetation treatments have clearly defined hydrologic consequences, but with other uses and treatments we have little more than clues as to their hydrologic effects, so there is need for additional study of hydrologic and physiologic processes, such as evapo-transpiration and water yields, and for more research to yield quantitative results for entire watersheds ("catchments" in British parlance). Such research will be time-consuming and costly, and most results can be applied safely and quantitatively only to areas similar to that where the research is done.'

The author deals faithfully with the climates, the topography, and the vegetational types in the U.S.A., then with the hydrologic processes as affected by vegetation and by structural works such as check-dams, contour ridges, contour ditches, and all the armoury of the soil conservationist. Part 3 which occupies more than half of the 400 pages deals exhaustively with the chief land uses, namely crops and their rotations, grazing, and trees, and with the effect of fire on the various types of chaparral, brush, and grass where fire is a major influence. Practically all the run-off and erosion data obtained by American workers since 1912 have been discussed and assessed in this context, but the only European work mentioned is Engler and Burger's Emmenthal experiment. India's contributions are not mentioned. One curious omission from his American references is C. F. S. Sharpe's *Landslides and Related Phenomena*, Columbia University Press, 1938, surely an outstanding contribution to erosion literature.

On the vexed question of the effect of tree cover on run-off and stream behaviour, the author differentiates firmly between the West, with its summer droughts and forest confined to mountains, and the East where there are no such distinctions. Only in the West do the fringing forests of the stream-side use any undue amount of the available water, and in view of the erosion menace he considers them a good investment.

Measurements of water flow and silt load show the superiority of undisturbed forest, particularly where rain intensities are high and soils are easily eroded. Porosity and water absorption rates decrease under the influence of felling, fire, and disforestation. In regions of heavy snowfall the removal of forest cover raises peak flows to dangerous heights by increasing snow-melt rates and reducing evaporation, rather than by causing an increase in surface run-off. J. E. Church suggested in 1912 that the maximum accumulation of snow on the ground with minimum melting rates would be achieved by growing (or cutting) forests so as to leave small openings surrounded by trees. As most of the Scottish hydro-electric catchments are around 2,000 feet elevation and completely wind-swept, this observation might be of interest to our water engineers, even when they insist that they have no silting problem at those high elevations at which they are now drawing their water power.

One has studied in the past the alarming effects of single storms such as the La Cresenta flood of 1934 in Southern California, when a million cubic yards of sand and debris poured from the mouth of a 20 square mile catchment, and the Davis County canyon of Utah carrying 300-ton boulders out into the orchards below. The average Britisher has read of these with the comforting feeling that such things only happen abroad. But what of the recent Lynmouth catastrophe which drove 50,000 tons of debris out of a 38 square mile catchment on Exmoor? Then there is the spectacular damage done by other single storms, such as those of Berwickshire in August 1948, Aberdeenshire in January 1953, and Eskdalemuir in June 1953. Should it not be apparent from these examples that river behaviour is of more than academic interest? E. A. Colman's book is indeed worthy of close study. And in view of the lamentable scarcity of accurate data for British river régimes, should we not be making a start with research on the lines he advocates?

Die Ertragsleistung der Nadelhölzer in Großbritannien und in Deutschland (Growth and Yield of Conifers in Great Britain and Germany), by R. Schober. *Forstwissenschaftliches Centralblatt.* Volume 74 (1955), No. 1/2, pp. 36–59, 8 tables, 7 figures.

Review by R. Lehtpere

BRITISH Yield Tables have aroused considerable interest in Germany and in the past they have been reviewed by Schwappach and Gehrhardt and more recently by Weck. In the present paper Professor Schober of Göttingen compares the *Revised Yield Tables for Conifers in Great Britain* (F. C. Hummel and J. Christie, Forestry Commission, Forest Record, No. 24, 1953) with German Yield Tables and, as he has had access to British results which have not yet been published, his paper contains information which will not become available to English readers until a new Forestry Commission Bulletin has been published.

He considers that up to an age of 75 years we may ignore the error caused by the differences in the method of measurement; in Britain only the stem volume is included whereas in Germany 'Derbholz' includes the branches which are more than 7 cm. in diameter.

British thinning grades appear to be heavy, especially at the younger ages, and, on the basis of numbers of trees per acre, the German C grade is somewhat lighter than our C grade. Little difficulty is caused by the British method of using the top height as a basis for quality classes in place of mean height which is used in Germany. Schober describes the method, which the British authors have employed, of preparing 'Master Yield Tables' in which all other measurements are related to top height, and then constructing the table for each quality class by inserting appropriate top heights at the respective ages. In this connexion he refers to Assmann's work which demonstrates that at any given height total production may vary within wide limits.

Volume growth in Britain appears to be extremely rapid. At 50 years quality class I Norway spruce has a mean annual increment which is 65 per cent. greater than that shown by Wiedemann's tables for North Germany with the same height, and quality class V Sitka spruce compares closely in M.A.I. with quality class I Norway spruce in Germany.

At 50 years the height growth and M.A.I. of quality class I Douglas fir in Britain are one and a half quality classes above quality class I in Germany according to Konzow, but the C.A.I. in Germany does not appear to fall off so rapidly as it does in Britain. Schober compares the tables for European and Japanese larch with his own tables for Germany and the differences in these species are relatively small. The M.A.I. in British quality class II Scots pine is about 50 per cent. higher than in tables by Zimmerle with similar height growth, and the M.A.I. of quality class I Corsican pine at the age of 50 years is double that of quality class I Scots pine in North Germany according to Wiedemann. Schober discusses at considerable length the reasons which may account for the superior rate of growth in Britain. He attributes it mainly to our oceanic climate—the long growing season, high rainfall, and high relative humidity. These are important reasons but we must also remember that many of our coniferous plantations are a first generation after hardwoods, that they have been carefully protected against vermin and have suffered little from diseases. Schober does not mention the difference that in Britain the age of plantations is counted from the year of planting whereas in Germany it dates from germination.

More information will be available to British readers when the Bulletin on the Yield Tables has been published. We shall then know the proportion of the sample plots of each species which belongs to each quality class and we may find that, although exceptionally good growth is commoner in Britain than in Germany, there is less difference in the average volume increment. In the meantime Schober's paper is a source of considerable information which is not yet available to us.

HONOURS

Members whose names appear in the New Year Honours List include the President of the Society, Mr. W. E. Hiley, Director Woodlands Research Department, Dartington Woodlands Ltd. (C.B.E.); Mr. F. S. Collier, Forestry Advisor to the Secretary of State for the Colonies (C.M.G.); and Mr. H. C. Dawkins, Ecologist, Forestry Dept. Uganda (M.B.E.). To all of them we offer our congratulations.

CORRESPONDENCE

Thoughts on Yield Tables[1]

Mr. Osmaston's article 'Thoughts on Yield Tables' is one of a number of welcome indications of the interest being shown in the recently published *Revised Yield Tables for Conifers in Great Britain*.

As he points out in the footnote to his article, our yield tables were actually compiled by using top height as the independent variable. In fact, we started by preparing a table very like the one which Mr. Osmaston deduced from the published tables. From this 'master table', as we have come to call it, we prepared the conventional form of yield tables by reference to the top height over age curves indicating the quality classes.

The convenient correlation between top height and total volume production had previously been made the subject of a research note by Hummel and Brett which appeared in the *Empire Forestry Review* (vol. 29 (1), 1950, pp. 58–59) under the title 'A simple method of estimating volume increment in stands of young conifers'.

Our data also confirm what Mr. Osmaston deduced from the Indian yield tables for Deodar about the effect of thinning grade on volume and the form factor; generally, we have found little or no difference in form factor between comparable plots thinned to different thinning grades. Most of our plots, however, are still comparatively young and the position may alter when butt swelling begins to exert its influence in the heavily thinned plots.

Our yield tables were published without giving a description of how they were prepared in order to issue them as quickly as possible; this description will be published separately, together with the basic data and notes on comparable growth records from abroad.

Yours faithfully,

F. C. HUMMEL and J. M. CHRISTIE

SOCIETY'S NEWS

ANNUAL GENERAL MEETING, 1955

The 28th Annual General meeting was held at Keswick on the 18th May during the excursion to the Lake District. Mr. T. E. Edwardson's paper 'Amenity and Forestry' printed in this number takes the place of the usual account of the excursion and it remains only to thank the hosts and organizers for the excellent arrangements made. We had snow in the Lakes in May and many of the young crops on the hillsides were showing damage from the cold winds of the long winter. We hope that the summer which followed—surely the loveliest summer for a generation—has done something to set this right.

[1] *Forestry*, xxviii. 117–24.

[*continued from inside front cover*

The membership is divided into four classes, the respective qualifications being as outlined below:

FELLOWS: Subjects of the British Crown fulfilling all four of the following requirements: (1) A degree or diploma in forestry, &c. (2) Five years of practical experience in forestry, &c. (3) Having been a Professional Associate for 5 years. (4) Having had a thesis or published article approved by the Council. Annual subscription £1. 11*s.* 6*d.* (Twenty-five guineas for life.)

PROFESSIONAL ASSOCIATES: Subjects of the British Crown fulfilling any one of the following requirements: (1) A degree or diploma in forestry, &c. (2) Having made important contributions to forestry, &c. (3) Considered by the Council to occupy a post normally held by a holder of a university degree in forestry. Annual subscription £1. 1*s.* 0*d.*

PROFESSIONAL MEMBERS: Subjects of the British Crown resident in Great Britain, engaged whole time in forestry but not eligible for above classes. Annual subscription 10*s.* 6*d.*

ORDINARY MEMBERS: Persons or corporate bodies not eligible for any of above classes. Annual subscription £1. 1*s.* 0*d.*

Fuller details of qualifications may be obtained from the Secretary.

Only Fellows are eligible for the higher offices and for most seats on the Council, but one Councillor may be a Professional Associate and one a Professional Member. Office bearers and Councillors are selected by written nomination and postal ballot. Fellows and Professional Associates have full voting rights, but Professional Members have only limited voting rights.

LIST OF OFFICE BEARERS 1955–6 AND COUNCILLORS 1955–7

President:	W. E. HILEY, O.B.E., M.A., Dartington Woodlands Ltd., Totnes, Devon.
Vice-President:	A. P. LONG, C.B.E., B.A., Chatley, Martins End Lane, Great Missenden, Bucks.
Editor:	R. W. V. PALMER, B.A., Bannerleigh, Leigh Woods, Bristol.
Business Editor:	H. L. EDLIN, B.SC., Forestry Commission, 25 Savile Row, London, W. 1. Tel. REGENT 0221.
Secretary and Treasurer:	R. A. GALLOWAY, O.B.E., M.C., B.SC., Solicitor, 7 Albyn Place, Edinburgh, 2. Tel. CAL. 7402.
Auditor:	D. L. FERGUSON, 11 Carlton Terrace, Edinburgh, 7.

Councillors: while immediate past president, SIR ARTHUR GOSLING; *retire in* 1956 *but eligible for re-election,* SIR HENRY BERESFORD-PEIRSE, A. H. H. ROSS, PROF. H. G. CHAMPION, M. V. LAURIE, and JOHN MAXWELL MACDONALD; *retire in* 1957 *but eligible for re-election,* G. W. BACKHOUSE, J. E. GARFITT, R. H. HIDE, W. M. MCNEILL, and PROF. E. C. MOBBS.

CONTENTS

Frontispiece. Afforestation in the Lake District (*Plate I*) . . .

The Discussion of Forest Problems. By W. E. HILEY 1

George Loyd Courthope: an Appreciation. By W. L. TAYLOR . . 4

The Distribution of Moisture in the Living Stem in Sitka spruce and Douglas fir. By L. CHALK and J. M. BIGG 5

The Composition of Tree Leaves. By J. D. OVINGTON 22

The Hybrid Larch. *Larix* × *eurolepis* Henry. By M. V. EDWARDS . . 29

Amenity and Forestry (*with Plates II and III*). By T. E. EDWARDSON . . 44

Growth Stimulation of Forest Tree Seedlings by the Activity of Free-living Mycorrhizal Mycelia (*with Plates IV and V*). By IDA LEVISOHN . 53

The Pattern of Mixtures. By L. C. TROUP and D. R. JOHNSTON . . 60

REVIEWS

Der heutige Stand unseres Wissens vom Humus und neue Wege zur Lösung des Rohhumusproblems im Walde (W. WITTICH), and

Mull and Mor Formation in Relation to Forest Soils (W. R. C. HANDLEY). By L. G. ROMELL 69

The Volume-Basal Area Line (F. C. HUMMEL). By H. M. STEVEN . . 71

Zeitschrift für Forstgenetik und Forstpflanzenzüchtung. Volumes I to IV. By J. D. MATTHEWS 73

British Mosses and Liverworts (E. V. WATSON). By E. W. JONES . . 76

Vegetation and Watershed Management (E. A. COLMAN). By R. MACLAGAN GORRIE 77

Die Ertragsleistung der Nadelhölzer in Großbritannien und in Deutschland (R. SCHOBER). By R. LEHTPERE 78

CORRESPONDENCE

Thoughts on Yield Tables (F. C. HUMMEL and J. M. CHRISTIE) . . 80

SOCIETY'S NEWS

Twenty-eighth Annual General Meeting, 1955 80

Printed in Great Britain at the University Press, Oxford, by Charles Batey, Printer to the University